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Volume XXVII - Fascicolo I

Biology as History

Papers from International Conferences sponsored by the
California Academy of Sciences in San Francisco and the
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N. 1

Systematic Biology as an Historical Science

Milano, 24-26 June 1993

Edited by Giovanni Pinna and Michael Ghiselin

MILANO 29 MARZO 1996

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Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano

Workshop on Systematic Biology as an Historical Science

PROGRAM

Thursday June 24th

9,00 Welcome address by Giovanni Pinna, Director of the Museo di Storia Naturale di Milano

Morning Session
Chairman: David B. Wake

9,30 Alberto Simonetta (Università di Camerino): Systematics: is an historical perspective useful to understand modern debates on systematics and are we really equipped for sound evolutionary systematics?

11,00 Alessandro Minelli (Università di Padova): Some thought on homology 150 years after Owen's definition.

12,00 Robert J. O'Hara (University of North Carolina at Greensboro): Trees of history in systematics and philology.

Afternoon Session
Chairman: Michael T. Ghiselin

15,30 David B. Wake (University of California, Berkeley): Schmalhausen's evolutionary morphology and its value in formulating research strategies.

17,00 James R. Griesemer (Wissenschaftskolleg zu Berlin): Some concepts of historical science.

18,30 Opening of the exhibition «Haeckel e l'Italia» at the Museo di Storia Naturale

Friday June 25th

Morning Session
Chairman: Adam Urbanek

9,30 Michael T. Ghiselin (California Academy of Sciences, San Francisco): Charles Darwin, Fritz Müller, Anton Dohrn, and the origin of evolutionary physicological anatomy.

11,00 Francesco Scudo (IGBE-CNR, Pavia): Symbiosis, the origins of major life forms and systematics: a review with speculations.

12,00 Mikhail A. Fedonkin (Russian Academy of Sciences, Moscow): The Precambrian fossil record: new insight of life.

Afternoon Session
Chairman: Cesare Baroni Urbani

15,30 Adam Urbanek (Polska Akademia Nauk, Warsaw): The origin and maintenance of diversity: a case study of Upper Silurian graptoloids.

17,00 E. Nicholas Arnold (The Natural History Museum, London): The role of biological process in phylogenetics with examples from the study of lizards.

Saturday June 26th

Morning Session
Chairman: Francesco Scudo

9,00 Yves Bouligand (Institute de Biologie Théorique, Angers): Morphological singularities and macroevolution.

10,30 Eugene Presnov (The Weizmann Institute of Science, Rehovot): Topological classification: onto- and phylogenesis.

11,30 René Thom (Institute des Hautes Études Scientifiques, Bures-sur-Yvette): Qualitative and quantitative in Evolutionary Theory with some thoughts on Aristotelian Biology.

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Cari colleghi
solo due parole per ringraziarvi di aver accettato di partecipare a questo workshop on Systematic Biology as an Historical Science, organizzato dal Museo di Storia Naturale di Milano e dalla California Academy of Sciences, e per presentarvi il nostro Museo.

Il Museo di Storia Naturale di Milano è un museo che, sebbene appartenga alla Città di Milano, è tuttavia il maggiore museo italiano di Storia Naturale.

Fondato nel 1938, prima dell'unità d'Italia, il museo ha avuto una lunga storia scientifica; in esso hanno operato alcuni noti studiosi italiani di ogni campo delle scienze naturali, che con le loro ricerche hanno fatto conoscere il museo anche al di fuori dei confini d'Italia.

Nel 1943 il Museo è stato completamente distrutto durante un bombardamento aereo, perdendo tutte le sue collezioni. Tutto ciò che oggi è presente nelle esposizioni e nelle collezioni scientifiche del museo è dovuto quindi all'opera di ricostruzione portata avanti con tenacia dalla città di Milano.

Oggi il Museo è in fase di ristrutturazione: si sta cioè operando per costruire un'esposizione più moderna e più informativa di quella realizzata frettolosamente negli anni 50, e che permise la riapertura al pubblico del museo dopo solo 7 anni dalla distruzione completa dell'edificio.

Prima di cedere la parola a David Wake, moderator di questa prima sessione del workshop, vorrei ringraziare Michael Ghiselin e Francesco Scudo, che hanno svolto una parte fondamentale nell'organizzazione scientifica del workshop.

Spero che avrete un buon soggiorno a Milano e tengo a precisare che le condizioni metereologiche non dipendono dall'organizzazione.

Giovanni Pinna

Ladies and gentlemen
Only a few words thanking you for your presence at this workshop on Systematic Biology as an Historical Science organized by the Museo di Storia Naturale di Milano and the California Academy of Sciences and introducing you our Museum.

The Museo di Storia Naturale di Milano, though depending on the Municipality of Milan, is however the most important Italian Museum of Natural History.

Founded in 1838 before the Italian unification, it has a long scientific history: here worked several well known italian scientists, whose researches in the different fields of natural history let know the Museum also outside the Italian borders.

During 1943 the Museum was totally destroyed by an air-bombardment, losing all its collections. All what is now present in the exhibitions and in the scientifical collections of the Museum is therefore due to the reconstruction work tenaciously pursued by the city of Milan.

Nowadays the Museum lives a phase of rearrangement, that is we are working to prepare up-to-date exhibitions offering more informations than those hastily carried out during the fifties, which allowed the reopening to the public only seven years after the total destruction of the building.

Before calling on David Wake, moderator of this first session, I am glad to thank Michael Ghiselin and Francesco Scudo, who played a fundamental role in the scientific organization of this workshop.

I hope you will have a nice stay in Milan, and I would like to specify that wheather conditions don't depend on the organization.

Giovanni Pinna

Fig. 1 - The participants to the Milano workshop. High up, from left: Alberto Simonetta, Michael Ghiselin, James Griesemer, Alessandro Minelli, Nicholas Arnold, Robert O'Hara, René Thom, Eugene Presnov, David Wake; below, from left: Giovanni Pinna, Yves Bouligand, Cesare Baroni Urbani, Adam Urbanek, Francesco Scudo, Mikhail Fedonkin.

Systematic biology as an historical science: discussion and retrospect

by Michael T. Ghiselin

Because the Milan conference was an informal gathering it did not seem appropriate to publish commentary by discussants. Instead the authors were encouraged to incorporate what had been said when they revised their manuscripts. A decision was also made to prepare a statement that would provide for some synthesis of the results. Ghiselin wrote a draft, based upon the commentary from the sessions and additional materials solicited from the participants. It was then circulated among the participants, revised in the light of their suggestions, and is presented here.

The intent of the organizers (Pinna, Scudo, Ghiselin) was to investigate some alternatives to the kind of phylogenetics that has recently become fashionable. The emphasis has been almost entirely upon cladograms and very little attention has been paid to phylogenetics in the sense of historical narrative. The very legitimacy of such an alternative has been seriously questioned. However, the intent of the participants was by no means to reject the advances in cladistic techniques that have become established in the past thirty years. It was a question of addition, not subtraction.

As someone who considers himslef a cladist, O'Hara expressed the opinion that opposition to narrative history and a broader range of evidence is becoming more and more a thing of the past, at least among younger workers. Simonetta, urged that the emphasis should be upon the questions raised, rather than upon particular answers. Minelli pointed out that narrative history is but one example of topics that have been underemphasized — especially comparative functional anatomy.

The diversity of the participants would probably preclude altogether any affort to found a new school of systematic biology. But their very diversity brought out how much opportunity has been neglected. If there was any unanimity about anything it was that lack of communication has been a serious problem. Work that might interest a wide range of systematists has frequently been known only to specialists in particular taxa, and the problem has been exacerbated by linguistic barriers. As O'Hara stressed, the work of systematists has much in common with a wide range of historical sciences. Furthermore, several of the participants have been seriously interested in the history of biology, and their presentations made it abundantly clear that a great deal of older work deserves more attention.

If any of the participants felt that philosophy is unimportant, they certainly did not give that impression. There were lively discussions about all sorts of philosophical issues, ranging from logical matters with respect to the definition and use of terms to the very foundations of metaphysics. For example, Thom suggested that the digestive tract is really outside of the organism. Some of the biologists (Minelli, Simonetta, Ghiselin), while acknowledging that this suggestion is legitimate from a topological pint of view, felt that it creates problems from the physiological point of view, especially when applied to various body cavities (such as the coelom being external in human females but internal in human males). The perennial discussion with respect to homology concepts cropped up with respect to «incomplete» homology (Urbanek). Arnold even went so far as to wonder out loud whether this term has been so vaguely defined as to warrant our abandonig it!. There was also some discussion about the appropriateness of other terms, for example, should we call a lineage that results from fusion of one or more independent lineages «polyphyletic»?

There was definitely no consensus with respect to such topics as the relative importance of form and function or pattern and process. The extreme difference of opinion might be summed up by saying that Thom supported the tradition of Pythagorus and Plato, Ghiselin that of Heraclitus, and Simonetta that of the nominalists. Griesemer extended this discussion by suggesting that process indeed deserves more attention, and it is not adequately understood either in developmental biology or in the study of how scientists do research. Wake raised the issue of whether heterochrony is pattern or process, and suggested that perhaps it is pattern at a taxonomic level, a notion opposed by Scudo on the grounds that development has to be a process.

Evolution, of course, is a process, but as Baroni-Urbani pointed out, there is serious question of how much evolution, if any, systematists really need when doing their work. One of the main reasons for holding the meeting was to address that particular issue. Nobody came out in favor of «pattern cladism» and maintained that systematists do not need evolution at all. On the other hand it seem unlikely that any of the participants will ever call themselves «process cladists» -- whatever that might mean.

Presnov's paper treated the evolution of echinoderms using purely topological characters, and therefore invoked only pattern. That this was a very interesting exercise was not disputed, and Ghiselin, who has done some research on echinoderm phylogenetics, opined that the results seemed quite reasonable given the characters that were used and that they could be supported by additional evidence. But he argued that he could have done the same job without translating the anatomy into topological language. Scudo said that the views of Presnov and Thom are

theoretically interesting, but that the practical significance is uncertain.

The metaphysical issue of the ontological status of taxa, including the proposal that species are individuals rather than classes, was not a major subject for debate. It did surface, in a sense, when Thom suggested that taxa are extensional sets and Ghiselin responded that they are composite wholes, which might better be treated with mereology rather than with set theory; they concluded that this was not the appropriate solution. Thom had asked about the tree of Porphyry, and O'Hara responded that there are important differences when we use a tree-like diagram to represent the relationships between abstractions such as kinds of furniture on the one hand, and historical entities connected by community of descent on the other.

The ontological notion of the individuality of species and clades (which, incidentally, Simonetta does not accept) relates to the epistemological issues that surround the role of laws of nature in historical inference. Laws of nature are generalizations about classes of individuals, and if taxa such as species are individuals rather than classes, it follows that laws of nature are not about taxa and the generalizations that systematists formulate about them are purely descriptions of contigent, historical fact. The principle of uniformitarianism in geology works because the laws of nature do not change. But since taxa evolve we cannot legitimately extrapolate to the past on the basis of features shared by all extant members of a group.

As Griesemer explains in his article, there has been a lot of discussion among philosophers of science as to whether the historical sciences are sciences at all. By defining «science» in the appropriate way, one can exclude such things as astronomy and mammalogy from the sciences altogether. Traditional philosophy of science has at least tended to downgrade history, including natural history, to an inferior status. And this makes a great deal of sense, since physicists founded the movement and naturally placed themnselves at the top of the academic pecking order.

But historical sciences, including not just zoology and geology, but astronomy as well, present more than just descriptive matters of fact about individuals such as the human species or the sun. O'Hara suggests that a distinction made by philosophers of history might be useful in this respect. Chronicle is a simple listing of events, whereas history proper is an explanatory account of suche events. As Griesemer points out, there are serious questions among philosophers of science with respect to the logic of historical explanation and inference, especially the role of laws of nature. Ghiselin in commenting on Fedonkin's contribution observed that in stratigraphic geology there are generally accepted and uncontroversial methodologies for establishing which event comes first on the basis of physical laws and principles, whereas in phylogenetics analogous modes of inference are often rejected.

The question naturally arises of what kinds of laws of nature or general principles might be used in the reconstruction of the history of life. There was general support of the analysis of embryology, but of course there have been a wide variety of embryological approaches to phylogenetics and other evolutionary studies. Darwin's application of what came to be called developmental mechanics to phylogenetic inference fits in quite well with mainstream evolutionary biology and there would seem to be no good reason to accept the claims of «Structuralists» that some kind of paradigm shift that eschews the theory of natural selection is in order (Wake, Minelli, Ghiselin). Wake and Ghiselin discussed this topic again after the meeting, when the question arose of how to differentiate modern notions of developmental constraint from traditional orthogenesis. And is there any real distinction between Vavilov's «homologous series» and Darwin's «analogous variation»?

One topic that was not explicitly addressed during the sessions, but did emerge several times during informal discussions, was the crucial role of museums in systematic biology. Because the workshop was cosponsored by two institutions that combine research with education, such issues were of more than just academic interest. The general public tends to think of natural history museums as something like art museums, the major role of wichich is to provide a chance for people to look at things. Their crucial role in research is most inadequately appreciated. Griesemer noted that museum displays are intended to show a particular order, but that there is a distinct gap between discourse and research. In meeting the demand for information about the environment, museums are reorganizing their public displays in a manner that tends to divert attention from the basic mission of systematics.

Systematics is of course the science that specializes in biodiversity, and therefore it has a crucial role to play in efforts to cope with the present crisis. During conversation, however, Wake expressed some concern about the study of biodiversity being dominated by ecologists, whose agenda is not necessarily compatible with that of systematists. There is a danger that systematics will be downgraded to a kind of service function for ecology and that, in consequence, it will lose the hard-won intellectual respectability that derives from its fundamental contributions to evolutionary biology.

The current prosperity of paleobiology exists largely be cause paleontologists were dissatisfied with the traditional role of their science as the «handmaiden of stratigraphy» and shifted the emphasis to matters of more general intellectual significance. The journal *Paleobiology* was established after a symposium on «Models in Paleobiology» held at the meeting at the Geological Society of America on November 2, 1971, in a deliberate effort to break with that tradition. The Milan workshop was convened with similar goals in mind, but with an important difference. The problem is not so much a matter of gaining autonomy for systematics, as it is of maintaining that autonomy by the continued exploration of new ideas.

E. Nicholas Arnold

The role of biological process in phylogenetics with examples from the study of lizards

Abstract — Biological process (except sometimes ontogenetic change) is not considered in cladistic phylogeny reconstruction using non-molecular characters, but such universal exclusion violates the principle of parsimony. Simple character pattern is often insufficient on its own to produce robust hypotheses of phylogeny, and extinction and congruence among what are in fact non-ancestral resemblances can cause misleading results; consequently additional insights from process are valuable. Process can be helpful in the recognition of character states, character independence, sequence of change in transformation series and among different characters, and in weighting, that is the assessment of the relative lability of character states. The fact that suppositions about are sometimes wrong and that their inclusion perturbs the basic simplicity of the cladistic approach are insufficient reasons for not considering them at all.

Weighting can be based on character compatibility, homoplasy in the studied group and outside it, and evidence of lability from trait variation and from possible selective interactions between organisms and the environment. The case for weighting is strongest when some or all these factors are correlated. Weighting is most appropriately used after the establishment of an initial cladistic pattern, to resolve conflicts in evidence, to asses robustness of phylogenetic hypotheses and, in principle, to assess relative transition probabilities for maximum likelyhood treatments of data. An example of weighting among lacertid lizards is given. Some of the evolutionary assumptions involved in weighting are testable using robust hypotheses of phylogeny based on character distribution alone and such tests can potentially provide some circumstantial evidence for the ubiquity of natural selection in evolution.

Inclusion of process in estimation of phylogenies can lead to circularity if the latter are subsequently used to study process itself. However, the extent of this problem has been exaggerated: where circularity is a real possibility, such studies can be safely conducted on robust phylogenies based on character distribution alone or ones that have been customised by removal of the specific process considerations concerned.

Introduction

This paper considers some of the possible roles of biological process in reconstructing phylogenies. In this context, process includes the changes that occur during ontogeny and the genetic and epigenetic mechanisms that produce them, functional interactions between traits constituting organisms, and functional interactions between organisms and their environment. Discussion will concentrate on non-molecular data.

Over most of the history of systematics, the idea that consideration should be confined to characters themselves would have seemed strange to most taxonomists and information or at least assumptions about process was often included. Thus Cesalpino (1583) gave precedence to traits involved in reproduction and nutrition and Cuvier and Darwin used functional considerations in weighting characters (Mayr, 1982; Darwin, 1859). In contrast, a widespread view over the past dozen years is that the appropriate way to conduct systematic studies is to take characters, recognise at some stage their derived states and, giving these equal weight, produce the most parsimonious hierarchical pattern associating taxa in terms of number of state changes (steps) involved. At no stage are general models of how evolution occurs or, indeed any suppositions about evolutionary process, allowed to impinge on the production of this pattern which can be used directly as a classification and, merely by a change of viewpoint, as a hypothesis of phylogeny. So, without any alteration, the hierarchy with least steps is assumed to represent the result of the evolutionary process. It can then be used as a basis for assessing models of evolution and recognising particular evolutionary phenomena.

This cladistic view of systematics obviously has great appeal and has been widely acknowledged (Platnick, 1979, 1985a, 1985b; Farris, 1979, 1980, 1982, 1983, 1985; Eldridge and Cracraft, 1980; Nelson and Platnick, 1981). In fact it has variants. What is often termed pattern cladistics excludes any reference at all to evolution and its primary aim is to produce a general basis for systematics. In contrast, evolutionary cladistics incorporates the assumption that hierarchical structure is a result of descent with modification and phylogeny reconstruction is its primary aim (see for example Hennig, 1966; De Queiroz & Donaghue, 1990, for discussion). However, although these variants are likely to sometimes differ in the results they produce, they share the general features of cladistics and will be treated together here, unless otherwise specified.

When views become conventional wisdom (Galbraith, 1957), they are less likely to be subjected to critical scrutiny. Consequently, the claims of general systems, like cladistics, need to be re-examined from time to time. In the present context, this applies especially to the supposition that the most parsimonious hierarchies of equally weighted characters are the best, or at least most appropriate, estimates of phylogeny and that most biological process should be rigorously excluded from their production. This question will be addressed here, but not such matters as the appropriateness of cladistic pattern as the basis of classification.

Problems in using cladistic pattern as the sole source for phylogeny estimation

It is a substantial imaginative leap to think that genealogical history can be derived from the distribution of current characters among species. It is not a leap that systematists have always been willing to make (for instance many members of the pheneticist school) and depends to some extent on how we believe, or rather hope, evolution generally has taken place. For total reconstruction to be possible, sufficient new traits must be generated, speciation events must be uncommon by comparison and parallelism, convergence and reversal must not prevent or obscure the development of a hierarchical pattern of character change. If this is not universally so, we will be reduced at best to reconstructing areas of phylogeny with very different degrees of certainty and some regions not at all.

Looking at the results of using cladistic pattern alone, this rather pessimistic possibility seems to be the case. A few analyses of groups appear unequivocal, with all relationships strongly supported by numerous characters and little conflict in the evidence, and these can be accepted as they stand as robust hypotheses of phylogeny. But, in other cases, there may be many alternative equally parsimonious solutions and even more that have only marginally fewer steps. Furthermore the level of character conflict may be very high and alternative trees very different. Indeed it is possible for cladograms without conflict to be substantially misleading as estimates of phylogeny. For instance, situations can be envisaged where extinction turns what would otherwise be clear homoplasies into apparent evidence of relationship (Arnold, 1981) and this is demonstrable in real groups, for instance when fossils are excluded from analysis of amniote relationships (Gauthier, Kluge & Rowe, 1988).

Even without such confounding effects of extinction or inadequate sampling there is no reason to think a single most parsimonious hierarchy will always represent genealogy, especially as other hypotheses may be scarcely less parsimonious. It is sometimes said that characters reflecting genealogy will be hierarchically congruent, whereas homoplasious ones will tend not be so (see for example Farris, 1969). However, it is not uncommon for competing sets of congruent characters to exist (p. 000), indicating that homoplasy can be ordered. Finally parsimony analysis will produce trees from randomised data and can therefore suggest pattern where none exists. Randomisation (= permutation) tests (Archie, 1989 a,b; Faith, 1991; Faith & Cranston, 1991; Trueman, 1993) indicate that this is indeed often the case with real data sets.

The cladistic approach to phylogeny reconstruction may turn out to be the best that can be achieved but it frequently fails to produce robust results and it is consequently appropriate to consider using additional sources of inference, such as ones derived from biological process, if this can be justified. Alternatively, we might take refuge in the hope that eventually additional characters will be found that enable a robust hypothesis of phylogeny to be produced by straightforward cladistic means. This may happen, but it is not certain to occur and in itself is no reason why other relevant evidence should be excluded.

Another problem concerns the application of the principle of parsimony, that the simplest solution that the evidence allows should be accepted. In cladistics, simplest is taken to mean the version of events involving the least number of steps. However, it can be argued that the principle is not being properly applied (Arnold, 1981), for its use carries the proviso that *all* relevant evidence should be considered before the simplest solution is chosen. Clearly on this basis, if biological process provides additional indicators about the way characters change these should be taken into account.

In cladistics, so far as is possible, different characters are considered to be potentially equal indicators of relationship and changes between states equally likely. This democratic approach, (Arnold, 1981), is essentially a kind of weighting for which there is no supporting evidence. It might possibly be justified by the statistical principle of indifference, that in the absence of any reason to expect one event more than another, they should all be assigned equal probability as a matter of convenience (Keynes, 1921; Wilkinson, 1992). Certainly, there are situations where it is necessary to work like this, but to raise such a pragmatic working method to a rigid law of procedure, prevents our ever investigating possible sources of information that might enable us to assign different probabilities to changes in states. In fact, cladistic phylogeny estimation often involves tacit character weighting of other kinds, either in processing characters in particular ways, for instance treating multistate characters as either ordered or unordered or eliminating characters on the grounds of their variability (Piementel & Riggins, 1987).

Some arguments against incorporating process

Supporters of the pattern-process dichotomy will often point out that their system, in eschewing most process, has the advantages of universal applicability, simplicity and clarity, for it is very obvious what is being done. Universality of application is a virtue in a method but not if it sometimes involves excluding other sources of inference that might otherwise be acceptable. In a country where vehicles are present but rare, there is little sense in insisting people should always walk merely because this method of locomotion is always available. While every effort must be made to achieve methodological clarity, other sources of inference should not be excluded on the grounds that they complicate procedure. Proponents of cladistic approaches also point to the efficiency of the hierarchies produced in reflecting information content but this does not necessarily indicate efficiency in reflecting phylogeny.

It is also stressed that it is easy to be wrong about process as an indicator in classification and phylogeny reconstruction. This is certainly true: Cesalpino was mistaken to believe that reproductive and nutritive structures of plants should be given precedence; some of Manton's (1977) arguments about the possible course of arthropod evolution based on limb and jaw function have not been supported by other sources of evidence. Although such cases are often emphasised, it must be remembered that cladistic patterns and the processes involved in producing them are also subject to reappraisal in the light of further

information, especially that derived from additional characters and taxa. It is inappropriate to exclude process indicators merely on the grounds that they are sometimes shown to be wrong; such exclusion is only justificable if such factors can be shown to frequently mislead. In phylogeny assessment, we are dealing with situations of general uncertainty: all evidence is provisional and this applies to the results too. The introduction of an additional set of faulted indicators into a system where pre-existing indicators are also faulted does not necessarily decrease overall reliability. Provided levels of failure are not too high and the new indicators are independent of those already present, they are unlikely to often generally reinforce errors associated with the latter. Instead, they can provide valuable corroboration of some hypotheses of relationships.

For a long time, knowledge of organisms was largely confined to their morphology which was accessible through museum collections, while information about other aspects was extremely sparse. In this situation, it was appropriate to concentrate on the anatomical features from which cladistic characters have been customarily drawn and it is not surprising that attempts to incorporate process were often clearly unsuccessful. However, now so much more is known about non-anatomical aspects of organisms, there is a much stronger case for attempting to use such information in phylogeny estimation and error is likely to be more avoidable.

At first sight, a more cogent objection to the use of evolutionary process, is the belief that including it in phylogeny reconstruction will result in circularity if such phylogenies are later used to study evolutionary process itself. In actuality, evolutionary process has many components and when studying one, the fact that other independent factors have been used in producing the phylogeny is immaterial. Furthermore for most uses to which phylogenies are put no such circularity exists. When it does so, it should be eliminated by modifying the evidential base for the phylogeny when such a study is made. Essentially, we have the alternatives of often accepting a suboptimal estimate of phylogeny based entirely on pattern which will inevitably frequently result in misinterpretation when investigations of process are based on it, or we can aim at the best substantiated phylogeny possible on all the evidence and then, if necessary, customise this for specific investigations.

It has sometimes also been said that the attempt to expose the hierarchical pattern of taxa and their characters is an important test of evolution, which would be lost if evolutionary process was not rigorously excluded from the procedure. Presumably, this is because a hierarchical structure is thought to be expected if both anagenesis and cladogenesis occur, but lack of hierarchy would not disprove evolution for it might be caused by excessive parallelism, convergence and reversal. Furthermore, the taxonomocentric view that hierarchy is especially important as support for evolution is wrong; most evidence comes from a combination of other sources such as the fossil record, the nature of the genetic mechanism and direct observation of short-term change in populations and intraspecific lineages. In fact there is no reason why simple cladistic hierarchies should not be generated separately from attempts to reconstruct phylogeny, if they are needed.

An alternative view of the relationship between hierarchy and evolution is that the former demands an explanation, giving a reason for invoking evolution to provide it (Panchen, 1992). Leaving aside the fact that a well marked hierarchy is often not discernible, it can be argued that the reverse is the case: evolution gives a reason why hierarchy is not unexpected and should be searched for rather than some other kind of order.

POSSIBLE ROLES FOR BIOLOGICAL PROCESS IN PHYLOGENY RECONSTRUCTION

It would be a happy coincidence if producing a hierarchical character distribution also automatically produced a phylogeny as a bonus, but as we have seen there is no real reason to expect this will always happen. This being so, it seems best to disengage any automatic association of character hierarchy, classification and phylogeny and aim for the latter as such, using whatever means are available including greater consideration of biological process.

Process is relevant in at least four areas of phylogeny reconstruction: recognising and specifying different character states, assessing character independence, determining order of state and character change and deciding which derived character states are likely to give more reliable evidence about relationships, that is character weighting.

Recognition and specification of states

Developmental studies sometimes show that features which are the same in their final form often have different early stages and this information can be used to recognise additional different states of a character (De Queiroz, 1985). Ontogeny can also indicate that a feature may be being misinterpreted. Thus, embryology suggests that the digits in the wing of birds are numbers 2, 3 and 4 and not necessarily numbers 1, 2 and 3, as their phalangeal formula in *Archaeopteryx* seems to indicate (Hinchcliffe, 1992). Developmental information, can allow character states to be defined more clearly. For instance, the limb pattern that delineates tetrapods may be better specified by the way it develops than by its highly varied final morphology (Hinchcliffe, 1992).

Assessing character independence

For characters to make an individual contribution to the establishment of relationships, they have to be evolutionarily independent of others that are used. Whenever derived states of different characters correlate in their distribution across taxonomic units there is the possibility that they are not autonomous and process information may be helpful in detecting whether this is so. For instance, evidence of shared genetic control can be searched for (Shaffer, 1986) and ontogenetic considerations of epigenetic interactions may also be helpful. In some salamander groups, the fifth hind digit is usually suppressed but develops when a large body-size is attained (Wake,

1991). Therefore these two features cannot be used as independent indicators of relationship. Ecological and functional cues may also be employed in this way. The various features developed by dune dwelling lizards that enable them to exclude sand from their body orifices are likely to be heavily selected for by this environment and consequently likely to evolve as a syndrome.

Sequence of change in transformation series and between different characters

Ontogenetic sequence is sometimes used for polarising character state transformations and many pattern cladists regard this 'direct' method of polarity assessment as more appropriate than outgroup comparison (Nelson, 1978). However, like outgroup comparison it is not a procedure that can be universally applied, since molecules and some organisms lack an ontogeny. Furthermore the claim that ontogeny is a direct method is true only of its observability and not of its relationship to phylogeny and its reflection of this. Total reliance on ontogenetic polarity determination would also mean that developmental sequences could not easily be used as different character states.

Ontogenetic polarity is assigned, either on the basis that primitive states are more generally distributed among adult and earlier stages of the taxa concerned (Nelson, 1978) or on the supposition that they appear earlier in ontogeny (Hennig, 1966). In terms of phylogeny reconstruction, the former is a special case of ingroup analysis (common = primitive) and suffers from the problems characteristic of this approach (Kluge, 1985). There is no reason to assume a priori that ontogenetic sequence will generally reflect phylogenetic sequence faithfully. This is something that can only be tested by comparing ontogenetic data for particular characters with the more direct phylogenetic inferences provided by outgroup analysis. Characters chosen for such comparison should have the assumed primitive state present in more than one immediate outgroup and direct and parsimonious transfer to other states in the studied group. Such comparisons suggest that de-differentiation, paedomorphosis and deletion of developmental stages sometimes result in misleading ontogenetic indications of phylogenetic polarity. Nevertheless, there is an often marked if incomplete congruence between ontogenetic and outgroup inferences. This being so, ontogenetic criteria might be used when outgroup information is not available, or is weak or equivocal. Confidence about polarity is increased when outgroup and ontogenetic information give similar results. However, when these indicators are both available but point in different directions there is no reason to give priority to the less direct indication of phylogenetic polarity provided by ontogeny.

Indications of the order of state and character change can also be gained from knowledge of how characters interact functionally (Arnold, 1981). To use such information in assessing polarity, it is usually necessary to make an assumption about how evolution proceeds. For instance, that new traits generally develop or at least become widely spread through populations in situations where a performance advantage is conferred. As will be argued, such assumptions are susceptible to independent test.

Labial scales in phrynosomatid sand lizards

The phrynosomatid lizards of North America show three basic patterns of upper labial scales: rectangular and flat; obliquely elongated with a diagonal keel; and obliquely elongated with a horizontal keel (Fig. 1a, c, d). Outgroup analysis suggests clearly that oblique elongation and keeling as such are derived, but it gives no indication as to whether keeling arose before or after elongation, or which orientation of keeling is secondary. Diagonal keels form part of a harmonious mechanism with obliquely elongated upper labial scales. Lizards possessing them, such as *Callisaurus* (Fig. 1c) evade pursuers by diving into often relatively firm sand. The head is oscillated rapidly about its longitudinal axis and the diagonal keels shave sand off the sides of the enlarging cavity into which the lizard moves. Oblique elongation of the upper labial scales increases the length of the individual keels and allows them to overlap horizontally, so the total length of cutting edge applied to the substrate is increased (Arnold, 1995). Making the assumption that traits generally arise in situations where they confer performance advantage, it seems likely that oblique elongation of the labial scales arose after diagonal keeling, since the former would not confer advantage in elongating the keels until these arose.
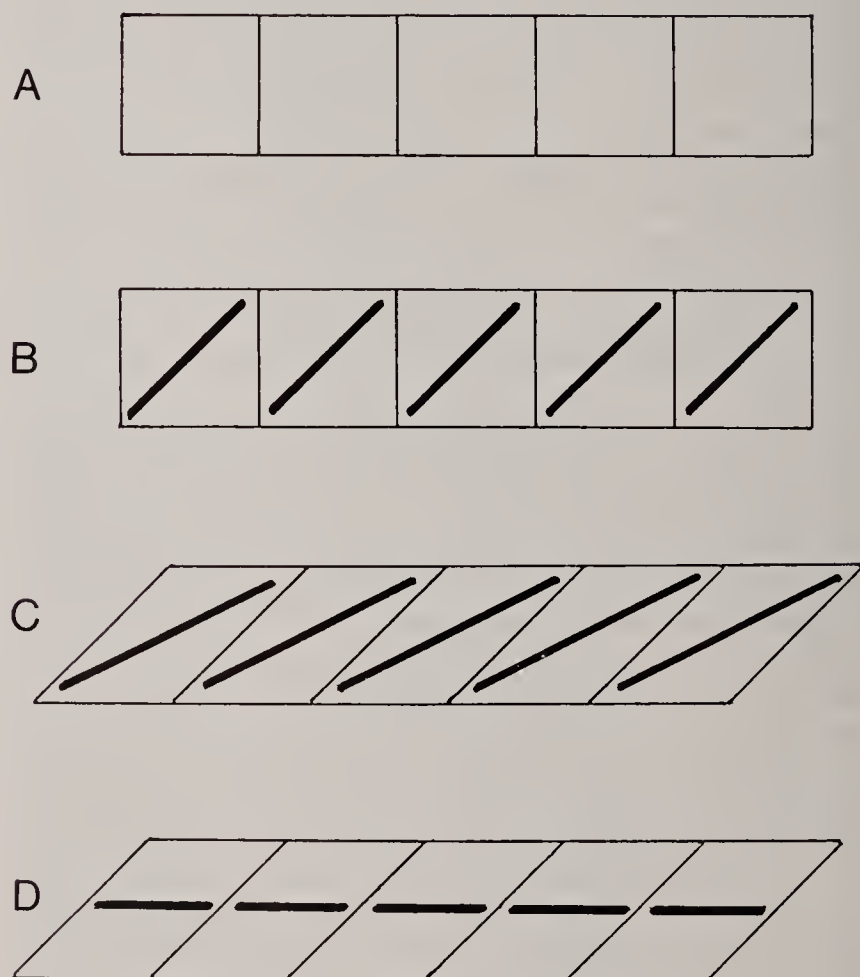
Fig. 1 - Diagrammatic representations of the upper labial scales of North American sand lizards (Phrynosomatidae); thick lines indicate keels. a. primitive condition (for instance *Sceloporus*) - rectangular and unkeeled; b. hypothetical condition - rectangular with diagonal Keels; c. derived condition (for instance *Callisaurus*) - obliquely elongated with diagonal keels; d. derived condition (nothern species of *Uma*) - obliquely elongated with horizontal keels. Functional considerations suggest that the evolutionary sequence was from a. through b. and c. to d, providing evidence that oblique scale elongation arose after diagonal keeling and horzontal keeling after this.

Horizontal keels on obliquely elongated scales (Fig. 1d) occur in species of *Uma* that burrow in very loose sand, partly by moving the head from side to side. The keels confer performance advantage by forming a lateral ridge that facilitates such sideways movement. In this situation, the oblique elongation of the labial scales has no discernible function, something corroborated by its absence in numerous independently evolved loose-sand burrowers. Functional considerations consequently strongly indicate that diagonal keels arose in the context of burrowing into firm sand, oblique elongation of the scales followed and finally the keels were reorientated to a horizontal position for use in soft sand.

It could be argued that events may have been more complex, for instance that oblique elongation of the scales arose in some other context and was only later co-opted to sand drilling. This of course is a possibility but, unless there is evidence for such greater complexity, the principle of parsimony should be applied, as for any other source of phylogenetic inference.

Gecko toes

Another example of the use of function is provided by the digits of gekkotan lizards. In different taxa, toes can be simple in structure without adhesive pads or internal muscles, or with both these features, or with one of them but not the other. There is consequently a classic incompatibility between two two-state characters (Le Quesne, 1969) (Fig. 2). It is apparent from outgroup comparison that absence of pads and muscles are the primitive states, so at least one character must be homoplasious, either having reversed or developed its derived state in parallel. However, it is not apparent which character this was, which of the two possible events were involved, and whether pads developed before muscles or vice versa.
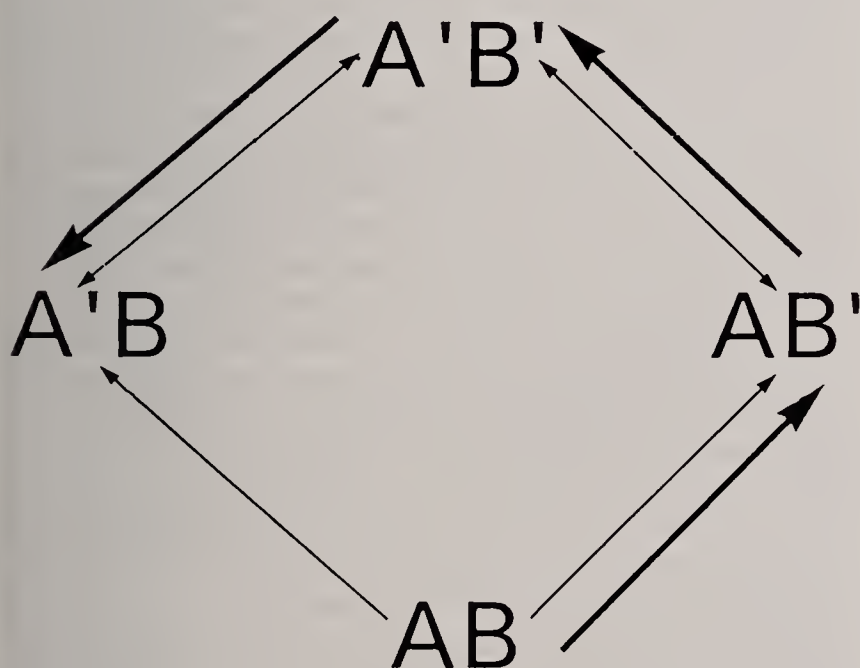
Fig. 2 - Conditions found in the toes of geckoes (Gekkota): A - no pads, A' - pads present; B - no muscles, B' - muscles present. These two binary characters exist in all four possible state combinations constituting a Le Quesne incompatability indicating that homoplasy must be present. Outgroup comparison establishes that A and B are the primitive states and thin arrows indicate possible directions of change. Functional considerations suggest that changes were as indicated by thick arrows.

Gecko toe pads confer performance advantages in many climbing situations by allowing adhesion to smooth and precipitous surfaces and there are many cases where they function without muscles. However, when muscles are present with pads, the former enable the adhesive mechanism to be used more precisely and the toes to be more easily detached, so that efficiency is increased (Russell, 1977). Species with muscles but no pads are usually ground-dwelling like many primitive taxa with neither of these structures and any benefits conferred by the muscles in this situation seem slight. If again traits are assumed to usually originate in situations where they confer a distinct performance advantage, it seems likely that muscles developed only after the origin of pads. Consequently, digits with muscles alone will have arisen by secondary loss of pads, rather than by independent origin of muscles.

As with ontogenetic cues, functional indications of order of state and character change can be used on their own when other lines of evidence are not available, or to increase or decrease confidence in decisions made on other grounds. This can be done before or after initial phylogeny estimation. In the examples just given, the functional assessments of order of change corroborate those found on phylogenies based on a wide range of other characters.

Functional considerations in ontogeny may also provide insight about order of character origin in phylogeny. For instance, if the presence of one trait is necessary for the development of another, it seems more likely that the former arose first. Of course this may not be so, for instance if the second trait was only secondarily developmentally dependent on the first, but provisional acceptance is appropriate.

Weighting

Since apparently derived states of different characters in a data set often suggest different relationships for taxa, some characters must be better indicators of relationship than others, unless all characters mislead. In this situation, it would be helpful to be able to distinguish states likely to reflect genealogical relationships from those where this is less probable. In attempting this we are frequently trying to determine the likely lability of derived states. An ideal marker of a clade is a derived state in which all possible changes involving it are unlikely (Fig. 3). This would mean that unique origin without independent developments was probable and that the state would persist without changing by reversal back to the original condition. Nor would it be likely to convert to an alternative derived state which other taxa have developed, or become unrecognisable by disappearance or further modification.

Weighting involves relative assessment of the probabilities of some or all of these transitions in different characters. Although low lability is likely to be frequent in informative states, it is also possible to envisage less stable traits that nonetheless give good information about phylogeny because their successive states specify a series of increasingly less inclusive clades. However, such features can often be treated as a nested series of stable characters.
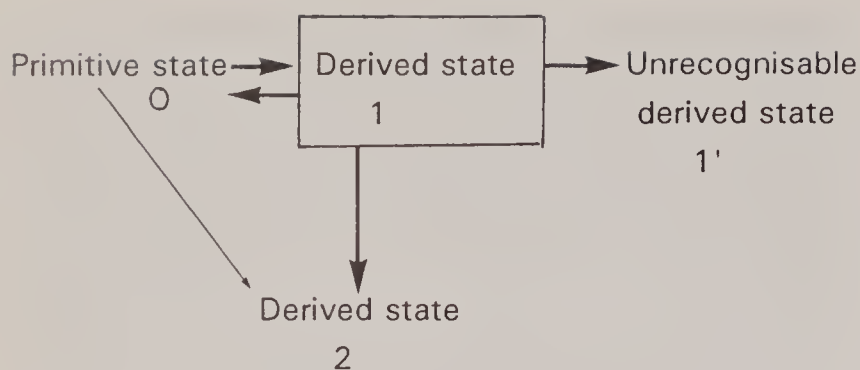
Fig. 3 - Some possible changes involving a derived character state (1). Its possible value in delineating a clade by all the members possessing it depends on the possession of low transition probabilities to other states. A perfect phylogenetic indicator would have a low probability of arising from the primitive state (0) thus restricting parallel development, and low probabilities of reversing to the primitive state, of changing to another derived state (2) causing convergence, or to an unrecognisable derived state (1') resulting in apparent absence. Most weighting indicators involve assessing some or all of these transition possibilities in a relative way.

1. Compatibility approaches. Le Quesne tests (Le Quesne, 1969) can be used to detect the presence of homoplasy in pairs of two-state characters and various procedures can be employed to recognise a clique of congruent characters and assign some kind of relative weight to the rest based on their perceived conflict (Gauld & Underwood, 1986; Sharkey, 1989). Such information can be used directly to form a hypothesis of relationship or employed as a character weighting system to choose among alternative trees produced by parsimony approaches. The use of compatibility methods in phylogeny reconstruction involves no hypotheses of process, apart from that evolutionary change occurs and that some characters are more labile than others. However, it should be borne in mind that, as in parsimony analysis, not all homoplasy will necessarily be detected so, on occasion, characters with fewer incompatibilities may be more homoplastic. Similarly, congruent cliques of characters are not necessarily the result of branching descent and may sometimes be due to convergence.

2. Homoplasy in the studied group. The idea that characters weight themselves by their congruence (Darwin, 1859; Patterson, 1982) can be applied after initial analysis. Characters that show more step changes at this stage can be regarded as being likely to be more labile than others and consequently downgraded before the analysis is re-run. The process can be repeated until a stable pattern is produced (Farris, 1969). An alternative approach is discussed by Goloboff (1993). Although evolutionary assumptions are denied for this successive approximations approach (Goloboff, 1993) there is a clear process expectation about the way characters behave: ones that exhibit apparent homoplasy are more likely to have produced homoplasies elsewhere than others.

3. Homoplasy in outgroups. Knowledge of outgroups may make it apparent that a particular feature has evolved, or been lost or modified in the same way, a number of times. This is suggestive evidence that the change concerned may be easily produced and consequently more than one appearance in the studied group is not unlikely. Such indications of multiple occurrence involve a process assumption, that similar organisms are likely to have similar propensities for particular character changes. The more cases of independent occurrence that can be recognised, the more closely related to the studied group and the more similar to it outgroups are, the stronger the case that such changes are likely to have occurred more than once in the studied group.

Conversely, certain features and systems, such as some genital characteristics, frequently give good information about relationships, judged by their frequent congruence with other characters. If this is so in immediate outgroups it is more likely to be so in the studied group.

4. Evidence of relative trait lability derived from the studied organisms

a. Variability of state expression in a wide range of taxa and lack of a clear gap between states can both be regarded as indications of potential lability. Experience with animal and plant breeding provides evidence that features which are variable or sub-continuous are often prone to change. Ideally, direct experiment on members of the studied group itself and its immediate outgroup could provide evidence of this lability, its likely universal occurrence in the history of the group and any bias in direction of change.

b. Evidence from developmental mechanics. Examination of the developmental process and experiment may provide evidence that some ontogenetic changes are more or less likely to occur than others; something that applies to shifts between derived states as well as their origins. If a series of traits are each developmentally dependent on the one preceding them in the sequence, the last are more likely to be lost than the first since so many others are dependent on these (part of the concept of burden - Riedl, 1979). As with variability, examination of taxa within the studied group and its immediate outgroup can provide evidence that such developmental characteristics are general.

5. Evidence of trait lability derived from possible selective interactions between the organism and the environment.

a. When there are multiple occurrences of a state in outgroups or the studied group or both, and these correlate with some aspect of the environment, it is likely that this aspect or some related factor exerts selective pressure for the development of that state, or at least favours its persistence, so that it is more likely to occur in that situation. For instance, the numerous independent developments of lateral fringes of pointed scales on the toes of lizards are nearly always associated with locomotion over fluid or semifluid media, especially aeolian sand (Luke, 1986).

b. The case for selective pressure for the development of particular states in a particular environments in enhanced if the way the change confers performance advantage can be discerned. In the above case, there is experimental evidence that the toe fringes prevent or limit sinking into the fluid medium concerned and thus improve locomotory capacity (Carothers, 1986).

c. Conversely functional interaction with the environment may provide evidence as to why certain transitions between states involving the same characters are unlikely to occur. Many flattened crevice-dwelling lizards have eyes that project above the skull but when they enter a fissure these are depressed and their lower section projects into the buccal cavity from which it is separated by a flexible membrane. However the way this occurs varies: in scincids and lacertids the eye projects through the suborbital foramen, while in cordylids it moves partly into

the interpterygoid vacuity. As these two openings are separated by bone, neither solution can be converted into the other without a loss of function. This would involve a reversion to the primitive condition where eye is unable to bulge into the buccal cavity.

d. Sometimes possible functional organ systems may have inherent characteristics that seem likely to affect their probability of change. Thus a case can be made that some genital features are likely to persist because they have to conform to those of the opposite sex and are also substantially buffered from environmental influences (Arnold, 1973, 1986).

Other weighting criteria have been suggested, for instance that complex characters are more likely to indicate relationships as they are less likely to evolve. However, direct knowledge of developmental mechanics of the feature concerned is likely to be a better indicator as to whether features are likely to develop in the same way and also of their likely persistence.

How should weighting factors and other inferences from process be used?

Not unexpectedly, the different weighting factors discussed often show correlation with at least some of the others. Such agreement of several factors is a much more convincing indication of potential evolutionary lability than any one indicator and should be looked for.

On occasion, there is a marked conflict in weighting factors, with compatibility and successive approximations methods largely supporting the initial results of parsimony analysis, while the other indicators largely based on biological process suggest an alternative phylogeny. In such a case the latter indicators should still be considered seriously since they are completely independent, differing entirely in their rationale from parismony, compatibility and successive approximations which all depend on ingroup character distribution.

Compatibility indicators can easily be assigned a numerical value (Farris 1969; Wilkinson, 1993) which could be used to weight character states either before or after parsimony analysis. Most other factors are relative and qualitative and it seems best to use them only when preliminary parsimony analysis has been completed (Arnold, 1981; Wheeler, 1986). They may then be employed to choose between alternative trees, particularly between those involving different sets of congruent characters. Another reason for applying weighting factors after initial analysis is that, while they may indicate which traits are more likely to give misleading information about relationships, they do not show that this is actually the case. Pontentially weak characters may sometimes indicate real relationships and should be given the opportunity to do so.

Even when parsimony analysis produces an unequivocal version of some or all the relationships constituting a phylogeny, weighting factors still have a potential role. They may be used to judge the degree of support for particular relationships by assessing the potential lability and independence of the characters delineating the clades concerned. This is not a substitute for statistical approaches, such as bootstrapping (Felsenstein, 1985) and permutation tests (Archie, 1989a, 1989b; Faith & Cranston 1991) but an independent source of inference.

An example of weighting in selected primitive lacertid lizards

Some characters varying among selected primitive lacertid lizards are listed in Table 1 and their distributions shown in Table 2. Parsimony analysis of the whole data set, using the Henning 86 program for phylogenetic inference (Farris, 1988) results in 31 trees of 59 steps and a consistency index of 0.50. A consensus tree produced by the Nelsen subprogram is shown in Fig. 4. This associates a group of species (A, C, E, G, I and K) in which all, or nearly all, of an assemblage of 14 characters (numbers 17-30) are present. Examination of the data set as a whole shows considerable conflict. When the group of strongly congruent characters 17-30 are removed, analysis of the remaining 1-16 shows that they too have strong internal congruence, a single tree of 21 steps and a consistency index of 0.76 being produced. As might be expected, this specifies a completely different pattern of relationships with the species previously associated by characters 17-30 being widely distributed though the tree (Fig. 5).

Table 1. Some characters varying among selected primitive lacertids; see Arnold (1973, 1989) for further details.

1. No pineal fontanelle.
2. Medial loop of clavicle continuous.
3. Medial expansion of clavicle restricted.
4. Arms of interclavicle directed obliquely posteriorly.
5. Sternum with a heart-shaped fontanelle.
6. Two pairs of diverging transverse processes on proximal autotomic caudal vertebrae.
7. Parietal scale extends to edge of parietal table of skull posteriorly.
8. Parietal table extends to edge of parietal table of skull anteriorly.
9. Supratemporal scale narrow.
10. Hemipenis with an armature.
11. Lobes flattened and complexly folded in uneverted hemipenis.
12. Hemipenial lobes long.
13. Hemipenial lips large.
14. Genital sinus unlobed.
15. Oviducts enter genital sinus at tip(s).
16. Ulnar nerve follows 'varanide' route.
17. Head and body depressed.
18. External nares of skull large.
19. Supraocular osteoderms fenestrated in adults.
20. Frontoparietal suture relatively simple.
21. Subocular foramen relatively large and rounded.
22. Dorsal scales flat and unkeeled and not markedly imbricate.
23. Collar beneath throat smooth-edged.
24. Ventral body scales more or less rectangular.
25. Ventral body scales not markedly imbricate.
26. Toes laterally compressed.
27. Toes markedly kinked.
28. Tail relatively fragile, usually with a high incidence of breakage and regeneration.
29. Dorsal colouring often uniform or with reticulate pattern.
30. Tail often blue, at least in juveniles.

Table 2 - Distribution of some characters varying among selected primitive lacertid lizards.

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Ancestral state	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
A. *Lacerta oxycephala*	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
B. *Lacerta laevis*	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
C. *Podarcis h. hispanica*	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	0	1	1	1	1	1	1	1	1	1	1	0	1	1	1
D. *Podarcis taurica*	0	0	0	0	1	1	1	1	1	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
E. *Lacerta perspicillata*	0	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1
F. *Lacerta andreanszkii*	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	0
G. *Lacerta cyanura*,	0	0	0	0	0	0	0	0	0	1	1	-	-	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
H. *Lacerta jayakari*	0	0	0	0	0	0	0	0	0	1	1	-	-	0	0	1	0	0	0	0	0	1.	0	1	1	1	1	0	1	0
I. *Holaspis guentheri*	1	1	1	1	0	0	1	1	0	1	1	-	-	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
J. *Adolfus alleni*	1	1	1	0	0	0	1	1	0	1	1	-	-	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
K. *Lacerta cappadocica*	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1
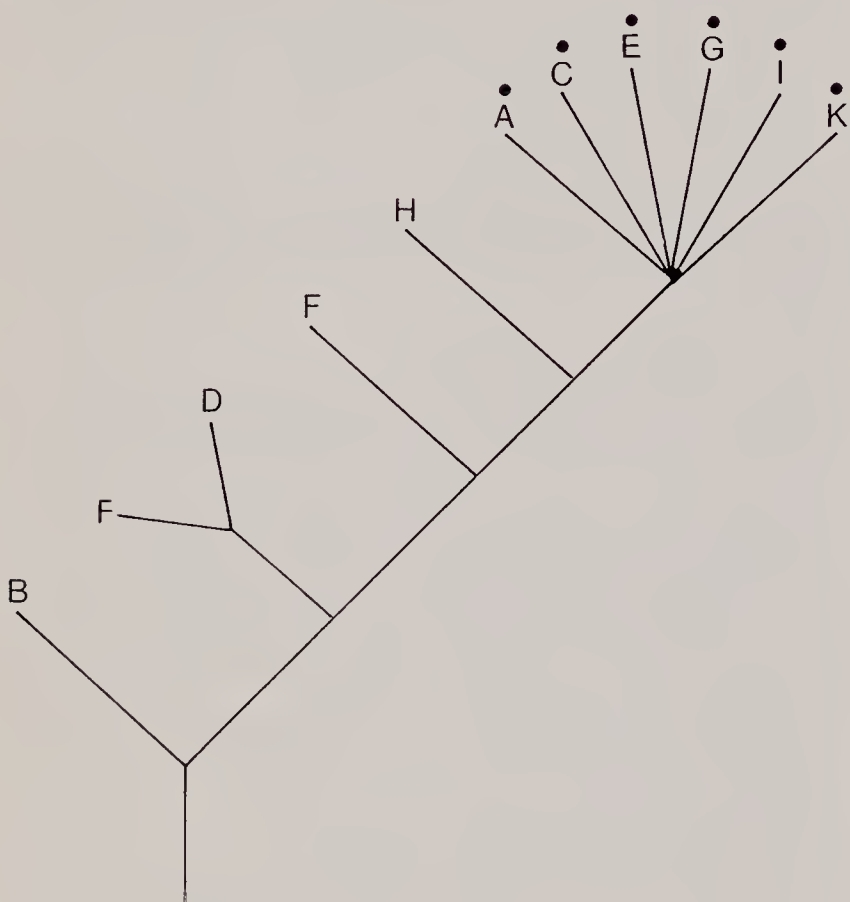
Fig. 4 - Relationships of primitive lacertid lizards based on 30 characters. Parsimony analysis associates species A,C,E,G,I and K (dotted) which share all or most of characters 17-30 (Table 1).
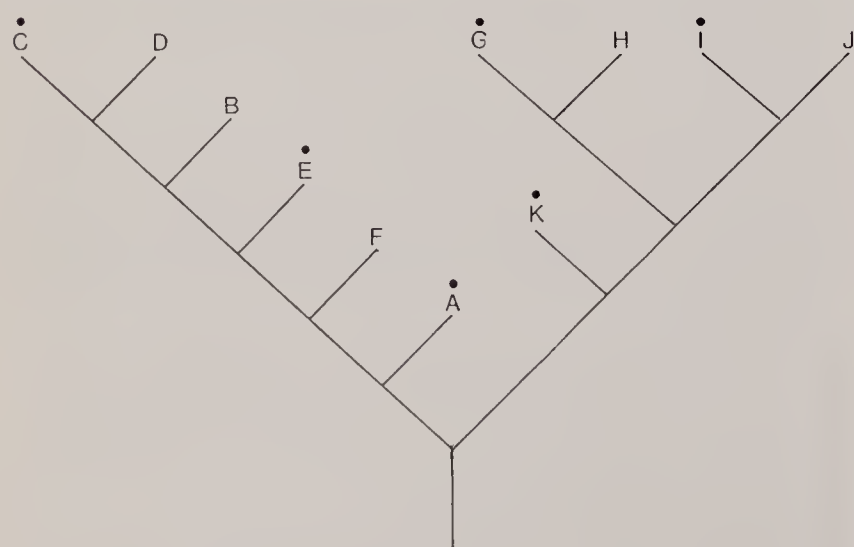
Fig. 5 - Relationships of primitive lacertid lizards based on 16 characters, excluding numbers 17-30 (Table 1). The apparent relationships of the six species associated in Fig. 4 (dotted). are now radically different. For further explanation, see text.

Cladistic methodology demands that the version of phylogeny involving all available characters and least steps should be accepted, but this would give no consideration to substantial conflicting structure that could represent genealogy and excludes relevant information about likely character labiiity. When possible weighting factors are considered, characters 17-30 that associate species A, C, E, G, I and K show far more of the indications of lability listed earlier. They are frequently intraspecifically variable, sometimes with the derived state not being abruptly separated from the primitive one, and many have evolved frequently in outgroups. Some osteological character states involve simple retardation of ossification. These characters occur, both in the studied group and in several outgroups, in a particular environmental situation in which they confer performance advantage, namely steep open surfaces with narrow crevices, whether rock faces or tree boles. Characters 17-25 are beneficial in using fissures, especially as refuges, 26 and 27 during locomotion on steep surfaces, and 28-30 in limiting predation (Arnold, 1973). In contrast, the remaining characters lack all or most of these indications of lability.

In this situation where conflicting sets of characters differ so clearly in weighting factors, there is a case for downgrading the set with strong indications of evolutionary lability and accepting the version of events suggested by the other. It might be predicted that if more characters are looked at, any that show strong congruence with characters 17-30 are likely to confer advantage in rocky situations.

Testing the assumptions involved in weighting and other uses of biological process

Some weighting factors involve relatively little in the way of premises, for instance compatibility approaches. Others merely assume that similar organisms and their attributes are likely to have similar evolutionary propensities. In the case of multiple occurrence in outgroups, this assumption is substantially self-testing, if a number of examples of independent origin exist. As noted, checking ingroup members and immediate outgroups can establish that a tendency to variability or a developmental characteristic is likely to have been present throughout the history of the studied group.

The main area requiring test involves evolutionary assumptions, such as that traits tend to develop in situations where they confer a performance advantage. Evidence for such a regularity includes the fact that a mechanism capable of producing it, natural selection, exists. Furthermore, this and an appropriate genetic system have been demonstrated in such a wide range of organisms that they may most parsimoniously be assumed to have been universally present during the evolution of contemporary forms.

A more direct way of investigating the generality of the assumption involves considering groups where simple parsimony analysis produces well substantiated hierarchies of taxa without much character conflict. As noted, these hierarchies can be regarded as robust hypotheses of phylogeny although, if desired other indications of robustness might be looked for, so long as they do not involve the assumption being tested. Such phylogenies can be integrated with information about the environments taxa inhabit and the performance advantages traits produce in the situations concerned. It is then sometimes possible to reconstruct changing conditions on lineages and see whether traits do actually develop at the times when they first confer benefit.

The lacertid lizard genus, *Meroles,* has a strongly supported phylogeny with its principal lineage extending steadily through a series of increasingly sandy habitats. No less than 70% of 61 shared derived binary characters appear on the main lineage at the points where they produce obvious advantage (Arnold, 1990). Included are features associated with locomotion on firm and then loose sandy surfaces, with diving into aeolian sand and its exclusion from the body, with sub-sand respiration and with camouflage on uniform surfaces. Such studies need to be carried out on as many robust cladistic phylogenies as possible to establish the generality of the assumption. As yet they have rarely been attempted but search for such a general correlation in time would provide a much more rigorous test of the importance of adaptation in evolution, than merely searching for contemporary correlations between traits and environments in which they produce performance advantage.

DNA base sequence analysis and the virtues of multiple approaches

The history of using DNA sequence as a source of phylogenetic information is illuminating. The development of this field has been substantially independent of the use of larger morphological features, yet it shows interesting similarities albeit on an abbreviated time scale. There was an initial optimistic feeling that most sequence was utilisable and its conversion into phylogenetic information would be straightforward. However, problems of analysis are considerable, congruence between different molecular phylogenies is often elusive (Patterson, Humphries & William, 1993) and some areas of sequence appear much more informative than others. There have consequently been efforts to recognise parts of the genotype that are more likely to be reliable, character weighting in effect. Thus, changes in functional parts of the sequence may be assigned greater significance because they are less likely to alter. For instance first and second base sites that specify amino acids making up proteins are often favoured compared with third-base sites. Relative probability of different kinds of changes between bases is also frequently taken into consideration. Transversions are often rarer than transitions and there are chemical reasons why this should be so; consequently they are often given higher weight. As in gross morphology, particularly complex molecular characters have been regarded as more reliable taxonomic markers because convergent origin is thought to be highly unlikely; for instance the BC1 RNA, a tRNA retroposon that may specify the Rodentia (Martignetti & Brosius, 1993).

Eclectic morphological systematists have sometimes felt a little smug about the increasingly perceived problems of interpreting DNA sequence. Some of them experience an unworthy twinge of Schadenfreude when watching people pay large laboratory costs to get into the same kind of procedural difficulties, that they themselves often managed for the price of a few scalpel blades, especially as attempts to amellorate the problems encountered often involve the same general approaches. But there are positive lessons that many morphologists can learn from DNA studies. In particular a willingness not to be tied to a single method of phylogenetic inference (see for instance Kim, 1993). As often portrayed, the pattern-process approach tends to be proscriptive, being presented as the only way of proceeding. This not only limits attempts to explore weighting methods that could be used in conjunction with it, but also precludes the employment of multiple approaches. If one method can be certainly recognised as superior in all circumstances then others can be discarded, but in phylogeny reconstruction this is by no means clearly the case. Available methods vary in the way they act and in the situations and ways in which they may fail. Cladistic parsimony approaches work well so long as change is relatively rare (Felsenstein, 1978), they tend to assign homoplasy to a wide range of characters and while they have the advantage of inevitably producing trees which usually have substantial structure, many alternatives may exist. In contrast, compatibility methods, although related to parsimony approaches (Felsenstein, 1988) tend to concentrate homoplasy in a smaller range of characters and, although they can be used to produce a single hypothesis of relationships, this often lacks complete resolution. In such a situation, where methods have different properties and are likely to reflect phylogeny better in different circumstances, there is a case for using all of them, unless there is evidence that they are clandestine versions of each other. Points of agreement will thus be more robustly supported (the principle of consilience - Whewell, 1840). Multiple methods have often been used in the history of science. For instance, acceptance of the reality of molecules and atoms depended crucially upon the remarkable agreement provided by more than thirteen independent methods that were used to determine Avogadro's number (M. Wilkinson, personal communication).

Another approach that is being put to increasing use in DNA sequence analysis is likelihood methods (Felsenstein, 1981). These require some estimate to be made of transition possibilities between the states

of characters, so weighting factors may eventually allow these methods to be broadly applied to morphological data, at least in limited form, and perhaps used in multiple method approaches.

Problems of using phylogenetics to study process

As already mentioned, one way of avoiding problems of circularity when testing assumptions of evolutionary process is to use robust unequivocal cladistic phylogenies that do not incorporate such assumptions. Alternatively, any process assumptions likely to produce circularity can be purged beforehand by eliminating them and reworking the remaining data used to produce the phylogeny concerned. However, many studies of evolutionary process do not involve real problems of circularity. For instance, because characters associated with rocky habitats were downgraded in estimating a phylogeny of selected primitive lacertids, it might be thought this would interfere with any attempt to look for a statistical correlation between such characters and those habitats in lacertids (the 'comparative method' of Harvey & Pagel, 1991). In fact, the rock characters were downgraded on a variety of grounds only one of which involved association with rocky habitats, so the latter could be discounted as to do so would not affect the results. Moreover, noting the association of character and habitat within lacertids did not in itself involve any hypothesis of multiple occurrence in the studied group.

The observation of multiple association, as an indication that the features were easily produced in rocky situations, applied only to outgroups. This being so, there is no vicious circularity in a later use of the 'comparative method' within the studied group if desired.

Some problems of using phylogenies to study process are essentially sociological. Until recently, phylogenetic studies were of principal interest to systematists but, in recent years, ecologists, ethologists and other biologists have become increasingly aware of the insights that phylogenies can bring to their work. While the development of such an audience is encouraging, it involves pitfalls.

There is a tendency for outside users to underestimate the frequently very provisional nature of phylogenetic hypotheses. It is not always realised that the best available hypothesis is often not very robust and very different almost as well substantiated alternatives may exist. Users may also fail to consider assumptions involved in constructing phylogenies that could lead to circularity in its utilizations. People employing phylogenies need to have enough knowledge of systematic procedure to be aware of potential difficulties and make some assessment of them.

Perhaps the relationship between the manufacturer and user of phylogenies should be like that between an ethical car-dealer and client. While the former should make potential problems clear, the latter must be willing and able to make more obvious checks on their own. As with vehicles, a reliable manufacturer is a start, but checks on mode of production and general robustness are very important. Finally, potential users need to ask hether the product really fits their specific needs as it stands and, if not, whether customisation may be a possibility.

Concluding remarks

The rigorous exclusion of most process from phylogeny reconstruction by cladistic means may have had the virtue of concentrating attention on many important issues, such as analysis of character transformation, algorithms and computer programs used in analysis, and the relative virtues of parsimony and other approaches. Now there is a consensus on some of these basic problems, or at least clarification of the arguments, there is a case for reconsidering the role of process.

Results of cladistic analysis suggest that it is often insufficient on its own to produce robust hypotheses of phylogeny. If such hypotheses are a primary requirement, it is appropriate to incorporate any other sources of inference that might improve this situation and can be justified, including many aspects of biological process. Proper application of the parsimony principle demands that such evidence should not be excluded and any insistence on rigorously avoiding differential weighting of characters cannot be substantiated on any grounds but pragmatism. That relevant process information is only sometimes available and is occasionally shown to be misleading is no reason for its rigorous elusion, especially as these shortcomings also apply to other sources of phylogenetic inference. Problems of circularity in using phylogenetic hypotheses, in which process considerations have been incorporated, are surmountable. Certainly, phylogeny estimation should not be automatically limited to parsimony analysis of characters on the grounds that this procedure has virtues unrelated to the task in hand, such as the information content of hierarchies produced or their appropriateness as a basis for classification.

It has been argued that *all* direct character data should be included in the assessment of phylogenies, if it can be sensibly integrated (Kluge, 1989; Eernisse & Kluge, 1993), and this principal of total evidence can be extended to encompass inferences on how characters are likely to behave during evolution. This also applies to using multiple indicators of order of change and of character weighting, and multiple methods of analysis.

In the approach suggested here, use of biological process occurs mainly after straightforward parsimony analysis so the basic cladistic pattern can still be recovered and used for other purposes. It might be pointed out that inferences from process are rarely made in practice and there is no consensus about detailed methods of procedure. This is presently so and results largely from the proscription of most process considerations in cladistic methodologies, but the process approach deserves to be explored further. It has the incidental virtue that the need for information on development and function and tests on assumptions about regularities in the evolutionary process will stimulate investigations in these areas. It may seem excessively laborious to consider such topics in phylogeny reconstruction, but these are valid subjects of interest in themselves and relevant to other areas of biology. The involvement of biological process in phylogenetics compares favourably in this respect with the drudgery of accumulating DNA sequence, the interest of which is largely limited to reconstructing relationships. It also helps confirm the central role of phylogenetics in integrating

different aspects of biology. Incorporating process considerations inevitably complicates phylogeny reconstruction, but there is no reason to expect that the recovery of genealogical patterns will always be simple.

In deciding how to perceive the world, there is a continuum of possibilities that may let us believe in fairies at one extreme but not even believe our own sense data at the other. Modest movement in the direction of increased scepticism is usually applauded in intellectual pursuits, especially when it manifests itself in overt procedural simplicity and rigorous rejection of what is perceived to be misleading evidence. Insistence on limiting phylogeny reconstruction to straightforward cladistic techniques is part of this trend but, in the long run, simplicity must not be bought at the expense of excluding relevant sources of inference. This is true even if such sources are faulted themselves, provided faults are not too common and independent of those in the original data set. While incorporation of biological process involves a move away from simplicity, its incorporation can be justified both in principle and practice. Thinking process is relevant in phylogenetics falls a long way short of believing in fairies.

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Morphological singularities and macroevolution

Abstract — Characters used in evolutionary studies lie at two extreme scales: *millimeters* or *centimeters* for instance in conventional systematics and *nanometers* in sequences of aminoacids or nucleotides. However, intermediate organization degrees do not escape natural selection. *Morphological singularities* belong to these intermediate levels and were defined by Rosin and Picken; they correspond to local rearrangements of tissue orientations and polarities, which belong to definite topological classes, as shown in figures 28 to 39. The evolutionary interest of these singularities comes from their likely role in organization and from the frequent differentiation of original organs in their core. Examples of such small organs are discussed in the case of a narrow and homogeneous family of parasitic Copepods, and also in larger groups, as Annelids with their characteristic bristles and Molluscs or other phyla, with closely related ultrastuctures.

The existence of morphological singularities is probably at the origin of difficulties encountered in the application of d'Arcy Thompson's method of continuous transformations. This theory preposes that limited changes in shape observed in development and evolution can be described with the help of a rectangular cartesian frame of coordinates, itself continuously transformed into a curvilinear grid; but it is clear that morphological accidents, as supplementary vertebrae or fingers, make impossible such continuous mapping from one individual to another one belonging to the same species. Singularities must be introduced in coordinates grids themselves to apply d'Arcy Thompson's methods.

More or less orthogonal arrays of fibrils exist in the integument of many vertebrates or invertebrates and show defined orientations in their anatomy. These fibrous lattices, which can be interpreted as a materialization of d'Arcy Thompson's coordinates frame, present singularities with original symmetries, someones being pentagonal. They were observed by Rosin (1946) in the basement membrane of amphibian tadpoles and more recently in the cuticle of marine worms (Lepescheux, 1988). These singularities create local specific morphologies, which resemble local simmetry breakings observed in liquid crystals, and this is quite natural, since self-assembly of fibrils is a morphogenetic process closely related to the phase transition involved in the transformation of an ordinary liquid into a liquid crystal.

Small causes produce important effects in non stable conditions and for instance, simple genetic events may interfere with hormonal regulations, leading to large morphological changes, as in heterochrony. Various kinds of *instabilities* occur at the level of morphological singularities, but instead of changes considered along the time axis, as in heterochrony, the relevant axes are those of coordinate grids. Such instabilities may intervene in the distribution of singularities over the whole body, or in the structure of their associated small organs, when they exist. We call *heterotopies* such processes and consider their plausible macroevolutionary consequences.

Introduction

Works on evolution deal mainly with two kinds of characters, considered at very different scales: 1. macroscopic structures, generally observed in the adult morphology and 2. genes or molecules, rarely used in current systematics. We pass from the visible phenotype to the less accessible genotype and we change the scale from centimeters or millimeters to nanometers. We learn which genes are involved in the expression of some essential morphological characters, but we still ignore the complex physico-chemical steps necessary for the elaboration of the corresponding characters in their whole structure. Many counterexamples can be proposed and some come from talks presented at this workshop, but much remains to study within the gap separating the phenotype from the genotype, despite the recent successes in developmental genetics.

Discussions are generally limited to these two extreme description levels and rather uncommon are evolutionary discussions on fine structures at intermediate levels, within cells and tissues for instance. Paleontologists rarely specialize in histology and their studies are limited to bones and teeth in the case of vertebrates. Histology is present in comparative anatomy, but there are few evolutionary investigations on tissues and cells studied for themselves and say at the ultrastructural level in general.

It appears that there is a large range of organizational levels, between nanometers and millimeters, which do not escape natural selection and present a high evolutionary interest, but are not generally considered from this point of view in the literature. Here also, counterexamples exist, but not too many, and the reason for this is possibly the general difficulty of correlating changes within cells and tissues with those observed in the environment, which also are described either in macroscopic terms or in molecular terms, the intermediate structural levels again being generally forgotten. However, such levels of description offer new aspects in the evolution of living beings, which could be narrated and integrated to this history, perhaps unique, of life at the surface of the earth.

A series of examples taken from my own works are now presented to show different difficulties I experienced in studying precise examples of evolution. Some mechanisms appeared to me as plausible, but were not discussed in my published papers, since I was unable to propose experiments or observations affording the beginning of a proof or of a refutation. All the considered examples will correspond in my mind to *macroevolution,* since they involve either changes which characterize higher groups, or changes within smaller groups, but however sharply defined. The concept of *morphological singularity* is due to Rosin (1946) and comes from the observation of the epidermal basement membrane in young tadpoles, as will be illustrated below. These singularities are also presented in the book of L. Picken (1960), with a general discussion on fibrous structures ob-

served in the integument of vertebrates and invertebrates. A morphological singularity can be defined as a narrow locus lying at the core of a rearrangement of the main orientations of certain tissues. Here, this term will be used in several examples, in particular for bristles in annelids and arthropods. The presence of one of these small organs creates a local rehandling within the structure of cuticle and epidermis, which can be interpreted as a morphological singularity.

Macroevolution within an apparently homogeneous family

Endoparasitic Copepods of Octocorals

Lamippids are parasitic copepods, a group of very small crustacea (generally 1 mm long or less) living in the digestive cavities or possibly in the mesogloea of *Octocorals* (Anthozoa, Coelenterata), these marine animals forming beautiful colonies of polyps with octogonal symmetries, the precious red coral being the classical example. When these endoparasitic Crustacea are adult, their morphology is deeply transformed and their wormlike body is then adapted to reptation within the host tissues (figs. 1-4), the morphology being grossly that of certain endoparasitic acarina, for instance, the common mites of the human skin, *Demodex folliculorum,* or also that of some mites in the family of *Eriophyidae,* living in the leaves of woody plants. When I began to work on these parasitic copepods with C. Delamare- Deboutteville, the main review on this family was due to de Zulueta, 1908-1910 (see references in Bouligand, 1966a) and represented an accurate systematic study, with clear conclusions:

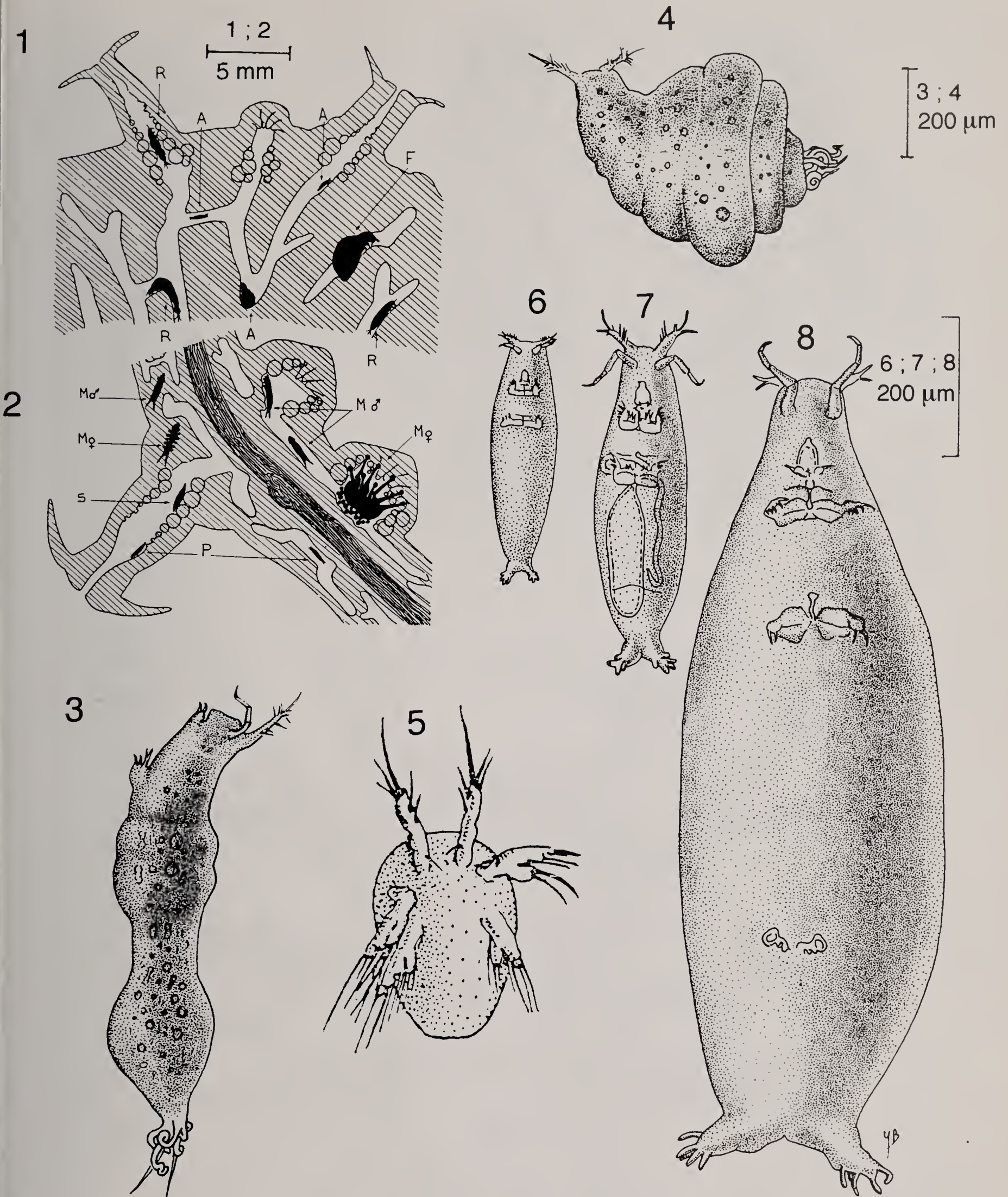
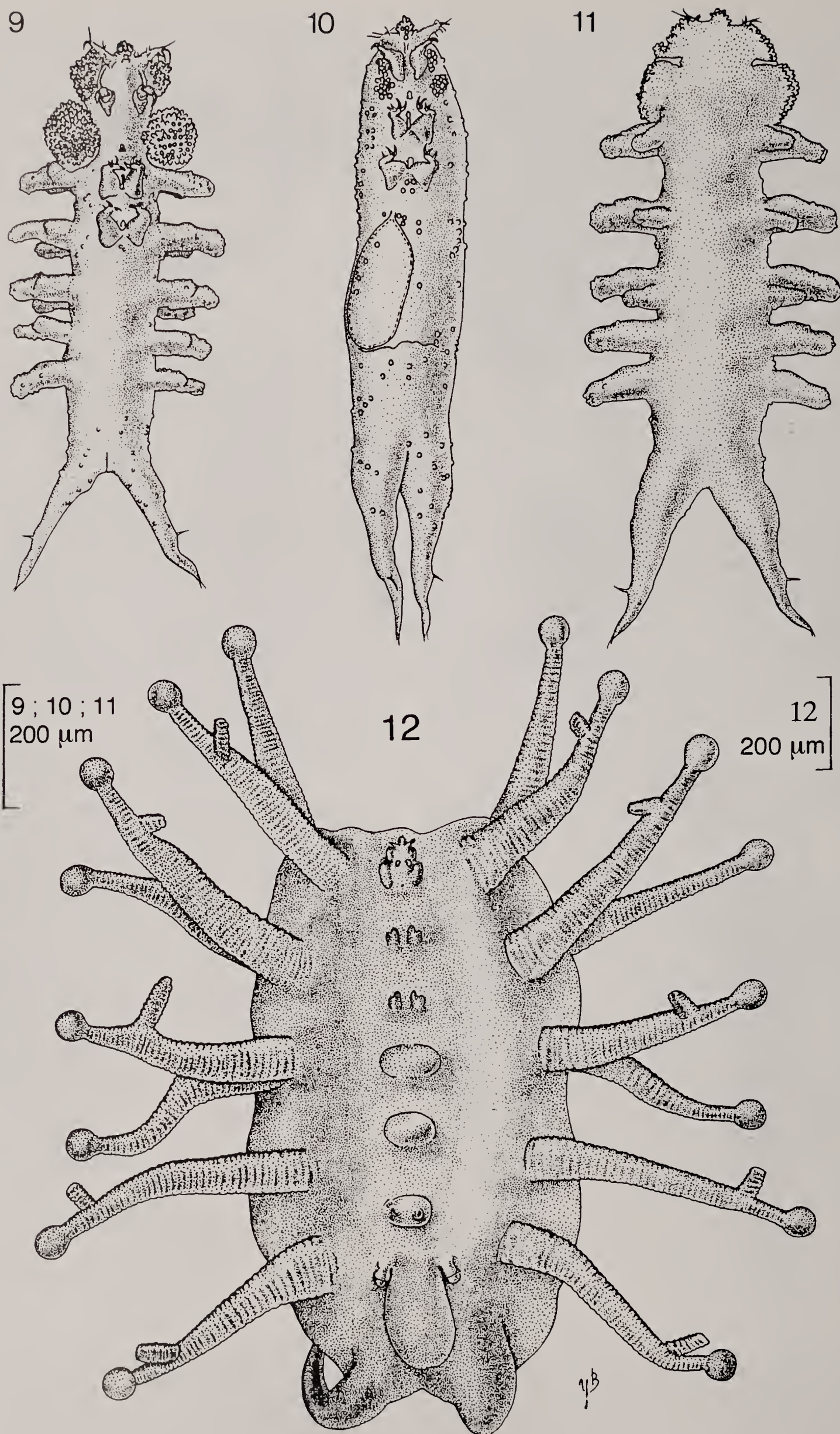
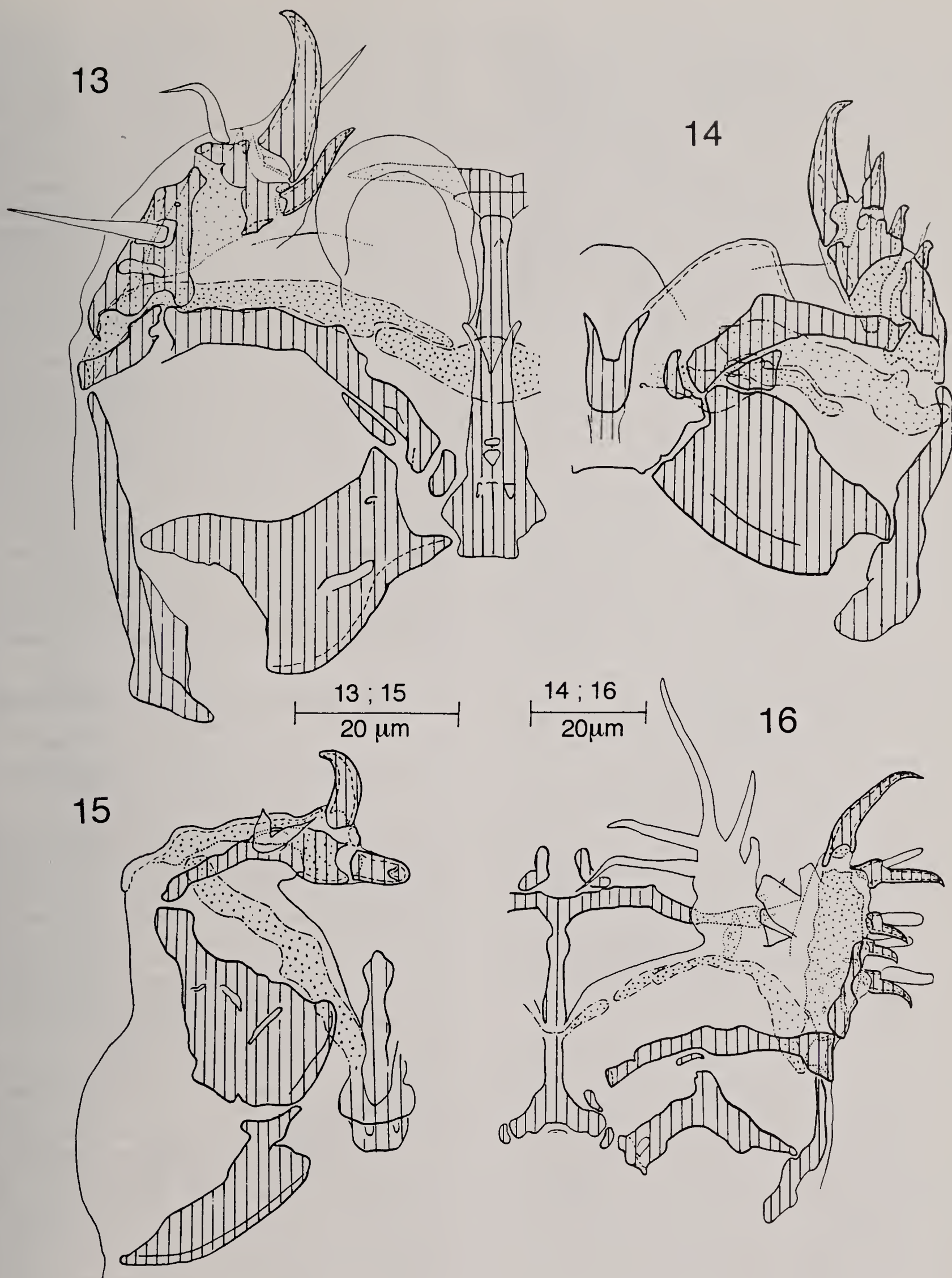
1. Most of the Octocoral species present in waters around Banyuls-sur-mer (Mediterranean Sea, near the frontier between Spain and France) are parasited, and each species of parasite is found in only one host. There are about fifteen known species of Octocorals in this area, but only twelve are parasited by Lamippids, and some of them by two different species of these parasites.
2. The morphology of each species is defined by recognizable microscopic characters of the four pairs of appendages and of the caudal furca.
3. The sexual dimorphism of Lamippids was said to be limited to the structure of genital apertures. The sex ratio was highly variable among species, one sex (either male or female) having never been observed for some species.
4. This family contained two genera, *Lamippe* and *Linaresia,* the second one with a unique species known only by its male. Some different species of *Lamippe* had been described from other seas, but either corresponded to species reviewed by de Zulueta or to other species with characters indicating a close relationship with this genus. This family was considered to be very homogeneous.

My observations made the situation much less clear, but can be summarized as follows:

1. Some new species were observed and someones suppressed with the agreement of de Zulueta (1961). An immature instar of reduced size, not much longer than the nauplius (fig. 5), was observed in several species, with the adult wormlike morphology, but without genital apertures (fig. 6).
2. The rule of host specificity of parasites was verified in general, but was less certain, since no morphological differences were found between individuals taken from some very different hosts. The parallelism between the two genealogies, that of the hosts and that of the corresponding parasites, suggested by the host specificity of parasites is not verified. There are many examples of closely related species found in phyletically distant hosts.
3. There are endoparasitic Copepods in Tunicates resembling strongly either the genus *Lamippe* (and that was already quoted by de Zulueta) or the genus *Linaresia.* These two genera possibly separated when they were parasites of Octocorals, but this is not demonstrated, since the host specificity is not so rigorous.
4. Examples of sexual dimorphism were also observed, some being slight, mainly a bigger volume of females (fig. 8). On the contrary, the female and the young females of *Linaresia* were discovered and presented an extreme sexual dimorphism (figs. 9-12).
5. The morphologies of the fifteen studied species (from Banyuls mainly) were drawn in great detail. The variations in the distribution of bristles or setae, within each species, are rare and were also described (about 10 anomalies for 500 observed specimens: addition, absence, or modification of a bristle).
6. The cuticle of these parasites is made of an homogenous epicuticle (soft, flexible and elastic in the genus *Lamippe*), observed on the whole body, and a rigid procuticle, limited to a set of sclerites present mainly at the level of the head, of the appendages, of the genital apertures and of the furca. The epicuticle alone forms the arthrodial membrane, which is extremely developed at the level of the thorax and the abdomen. A wormlike anatomy is reconstructed in the genus *Lamippe,* with circular and longitudinal muscles involved in peristaltic movements (Bouligand, 1966 a and b).

Visible macroevolution

The first half of this morphological study was published, but I never completed the manuscripts of the second half, simply because I tried to prepare a classification close to phylogeny, if possible, but I did not succeed. Several tables were established for characters varying as discrete entities between species and, in principle, the situation was good, but it was necessary to look for other species, and this was never done. I was only able with the available information to gather some species into subgroups and not to build a complete genealogical tree.

It was clear (but I still wait for a rigorous proof) that the strong sexual dimorphism, which was already visible in the young female of *Linaresia,* was secondary relative to the general morphology of Lamippids, present in males and in young females (except the lateral extensions already visible in these latter). It also appears that an extreme macroevolution is possible in this group, without affecting the main characters of the other instars, recognizable for instance in the morphology of appendages, and which give the best elements for a definition of the Lamippid family (fig. 13-16). The digestive system (mesenteron) is absent (or deeply modified) in the young female and in the adult female of *Linaresia,* whose cuticle is strongly thickened and crossed by a complex system of branched and anastomosed canals (Bouligand, 1966 a, b).

Figs. 1-8 - 1) Schematic section of an Octocoral colony (*Alcyonium palmatum*) with two expanded polyps and a smaller one in the middle, being retracted. Several Lamippids are represented in the canals of the coenosarc, but are much less numerous than represented: A: *Lamippe aciculifera* (adult or immature); F: *Lamippe faurei;* R: *Lamippe rubicunda.* 2) Similar section in the Gorgonian: *Paramuricea chamaeleon,* with one expanded polyp and two retracted ones. M: *Linaresia mamillifera* (immature or mature females and males); P: *Lamippe parva* and S: *Lamippe setigera.* 3) Drawing of *Lamippe rubicunda* observed alive, after extraction from its host (*Alcyonium palmatum or A. acaule).* 4) The contracted body of *Lamippe rubicunda.* 5) A lamippid nauplius observed in *Alcyonium.* 6, 7 and 8) Immature stage, male and female of *Lamippe aciculifera.*

Figs. 9-12 - *Linaresia mammilifera.* 9) Ventral view of a young female. 10) Ventral view of a male. 11) Dorsal view of a young female. 12) Ventral view of an adult female.

Figs. 13-16 - First thoracic legs of four different species of Lamippids. Hatched areas correspond to directly visible sclerites, whereas dotted structures represent other sclerites observed by transparency. 13) *Lamippe rubicunda*; 14) *Lamippe faurei*; 15) *Linaresia mammilifera*; 16) *Lamippe aciculifera*.

Less visible macroevolutions

The integument of these copepods presents many differentiations considered in figs 17-22. There are for instance several types of papillae as shown in fig. 21. There are two other characters, already described by de Zulueta, which separate two subgroups in the genus *Lamippe.*

The first one corresponds to species showing at the tip of setae, a bunch of needles (or *aciculae),* with refringent droplets slowly running along them, as for axopods of certain planctonic protozoa (Actinopoda). In some Lamippids, the aciculae are mainly observed at the furca (fig. 19), whereas in other ones they decorate all the appendages (fig. 20). In *Lamippe chattoni,* they cover the whole body, pointing outside, normally to the arthrodial cuticle (figs. 17, 18). I was convinced in the first years that this very unusual character was the signature of a synapomorphy, but it was not confirmed by the other morphological details of appendages, and I learnt that aciculae, possibly related to those of Lamippids, existed in other parasitic copepods of the genus *Pachypygus* living in tunicates (Hipeau- Jacquotte, 1986). These aciculae of *Pachypygus* are made of a bundle of parallel microtubules (as in Actinopods), an ultrastructure I still not verified in Lamippids, but in which I believe, since there are visible droplets moving along these aciculae, which were remarkably filmed by J. Painlevé.

The second character allowing one to separate a second subgroup within the genus *Lamippe* still holds and corresponds to another strange modification of setae, which are contractile, as shown in the figure 22. These slow deformations, also filmed by J. Painlevé, are due to myofibrils visible within these transformed setae, in histological preparations. I never heard of examples of this kind of structures in any other Arthropods. I spent days in libraries to find examples in literature of similar contractile setae (and also setae with aciculae). I have spoken of this problem with many colleagues. I suppose that the synapomorphy corresponding to the presence of contractile setae is genuine and I never changed my opinion. The other morphological characters confirm this synapomorphy. However, there are only three species in this subgroups and what had been experienced with the aciculae might reproduce with these contractile setae.

My hypothesis was that a very original character, common to several species within a family, is generally attributed to the signature of a common ancestor, but actually similar productions may appear independently in very different lineages. I suggest that this is simply because the expression of this character depends on the overstepping of certain thresholds and that this can be achieved by very different genetic situations. There are no means to verify such conjectures in the present context of genetic and molecular studies and this is particularly obvious for this sort of copepods. Current molecular research with such animals is not easy, since one generally finds them in small number and their dimensions also are very small.

Relativity of macroevolution

The three different evolutionary characters discussed in this family of copepods (strong sexual dimorphism, axopodlike aciculae and contractile setae) correspond, in my mind, to three examples of macroevolution. The first one appears as obvious from the direct examination of the external morphology, whereas, the two other ones are purely microscopic details, but very unusual.

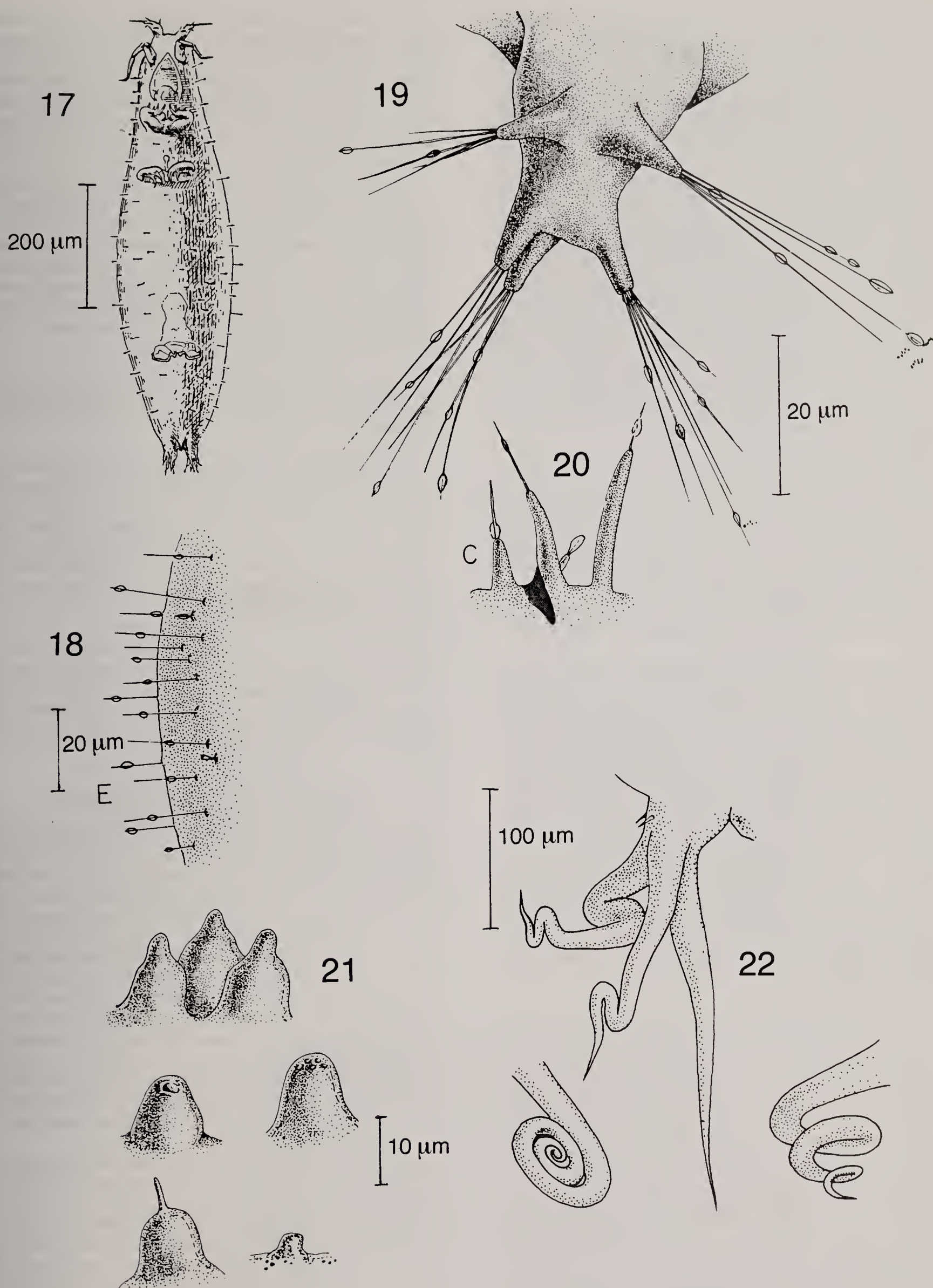
Considered at the histological level or at the ultrastructural level, these variations, within this narrow family of parasitic copepods, can appear as important as those we know in the whole phylum of vertebrates, from fishes to mammals. For instance, do we know examples, in vertebrates of such involution of the digestive canal, with a compensation through the skin, as in many parasitic worms? Several cases are known in other groups of crustaceans, namely *Sacculina,* described in handbooks of zoology. The difficult question remains to appreciate the genetic changes related to these extreme transformations. We can suppose for instance that genetic modifications were small with respect to their considerable phenotypic consequences, since the appendage morphology is not deeply transformed in males and in young females. On the contrary, we can think that, from the separation between *Lamippe* and *Linaresia,* which can be very ancient, the genetic evolution has been possibly considerable, with however few incidence on the appendage structure, since neutral mechanisms in evolution are also to be taken into account. Actually, there is no real hope to verify all that in the next twenty years, if I am not mistaken.

D'Arcy Thompson's theory and morphological singularities

Difficulties in the application of the theory of transformations

Since I had prepared numerous drawings of the appendages of Lamippids, I have tried to apply the method of continuous deformation due to d'Arcy Thompson, but I did not succeed. I still think that this method is based on an excellent idea, but there are difficulties. The book of d'Arcy Thompson (1917), entitled *On Growth and Form,* deals with geometrical and physical constraints faced by organisms in the course of development and evolution, but its main impact comes from the last chapter devoted to this theory of transformations.

Briefly, this theory proposes that one passes from the form of a given species to that of a related one, by a progressive deformation, which is that of a rectangular cartesian frame of coordinates into a curvilinear one, so that two small structures recognized as homologous in the two different species, have equal coordinates in the two arrays. I did not really obtain such continuous mappings between most species of Lamippids. The evident difficulty comes from segmentation and ramification of appendages. A simple explanation can be considered in the case of vertebrates: there are examples of supplementary vertebrae or fingers and such variations make the continuous mapping from one individual to another one impossible.

Like the teeth of mammals, all bristles of Lamippids can be given a name, and species are differentiated by the presence or the absence of some particular bristles (figs. 13-16). One can propose such continuous deformations only at the level of a series

Figs. 17-22 - Small organs in Lamippids. 17) *Lamippe chattoni*, with its cuticle covered by thin aciculae. 18) Enlarged view of aciculae at the surface of the cuticle of *Lamippe chattoni*. 19) Groups of aciculae emerging at the tip of some specialized setae in *Lamippe aciculifera*. 20) In the same species, isolated aciculae emerge from bristles of antennulae. 21) Papillae observed on the head of *Linaresia* and on the body of different *Lamippe*. 22) Different shapes observed with furcal retractile setae in *Lamippe rubicunda*.

of sclerified plates (or sclerites) well differentiated in the cuticle of the thoracic appendages (figs. 23-26). However, many problems remain unsolved even in this situation. Well identified sclerites, such as j and γ in fig. 23, disappear in some species (fig. 26). Others are added (fig. 24, α, β). What can we do with these sclerites which are either present or absent? For instance, we do not know whether or not the sclerite γ, present in figs. 23 and 25, is a piece of sclerite present at level d (fig. 24) or is different from it (fig. 26). Another problem is that of the relative proportion of arthrodial membrane, lying between the sclerites, which varies considerably between species. Compare for instance figures 24 and 26, and particularly the zone B,efg mainly formed of arthrodial cuticle in fig. 24 and mainly sclerites in fig. 26. Two opposite trends are observed in these two species. The sclerites resemble pieces of a puzzle in fig. 26, with little room for arthrodial membrane, whereas they form elongated rods in fig. 24, with a maximum extension for the arthrodial cuticle, and this trend is visible in all the parts of the body.

Since continuous transformations are impossible, singularities were introduced as shown in fig. 27, to take into account such discrete variations, as the introduction of a new bristle, but the problem is that there are several ways to do that, with a more or less arbitrary localization of singularities. It must be recalled that singularities were considered in coordinates grids, as possibly useful in the interpretation of experiments involving morphogens (Bookstein, 1981).

If some details are not taken into account, it is possible to draw separately the coordinate frames and their deformations, at different levels of organization. Each bristle can receive its own coordinates system, which resembles for instance the generators of a cone and the set of circles lying normally to generators. The comparative morphology of a definite sclerite can be treated by d'Arcy Thompson's methods. Difficulties arise with sets of sclerites and bristles, particularly when one is faced to the introduction or to the disparition of some of these elements. The problem is to insert smaller graphs within larger ones, in order to see the articulation between the successive levels, and this creates singularities, but nothing is really sure in the preparation of these coordinates systems integrating several different description levels.

I came back to the text of d'Arcy Thompson, to observe that probably he had himself encountered problems in the application of his method. D'Arcy Thompson compared a series of more or less direct ancestors of horses. The difficulties are implicit in legends to the figures representing the simplest series of transformations from the skull of *Hyracotherium* (Eocene) to that of *Equus* (contemporary horses) through «various artificial or imaginary types, reconstructed as intermediate stages», which are supposed to represent the direct line of descent. Skulls of *Mesohippus, Protohippus, Miohippus* and *Parahippus* are drawn for comparison with the imaginary skulls, but without their own curvilinear arrays. The study shows that *Mesohippus* and *Protohippus* are not far from being in the direct line of descent from *Hyracotherium* to *Equus,* whereas *Parahippus* corresponds to a somewhat divergent branch in the genealogy. If one tries to draw the absent array for *Parahippus,* it appears that strong local distortions are necessary for this skull. This is not due to the fact that the array is in two dimensions and difficulties would not be resolved with the use of three-dimensional coordinates systems. These difficulties could be much stronger, if we had the possibility to examine the original materials and the accurate drawing of suture lines of cranial bones.

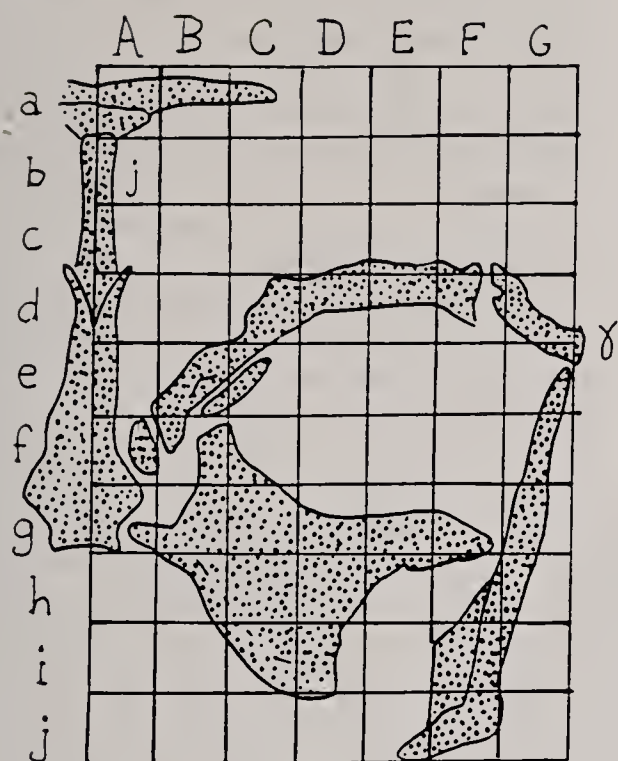
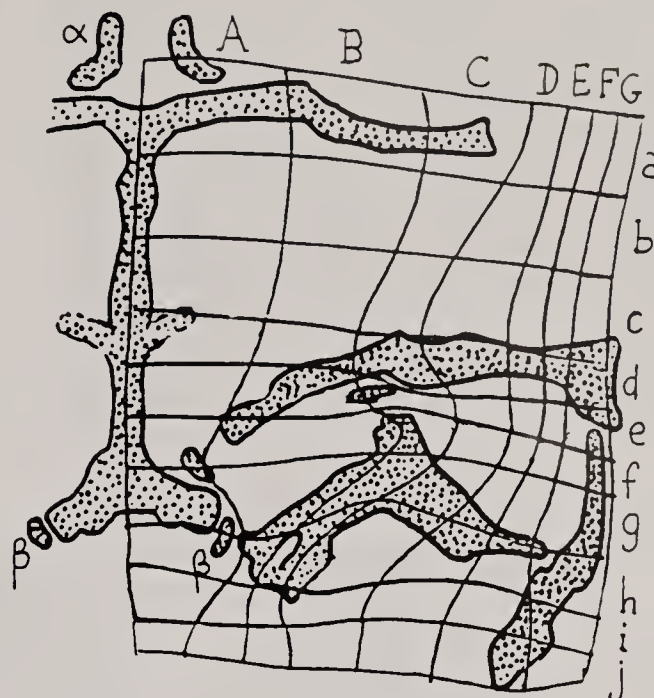
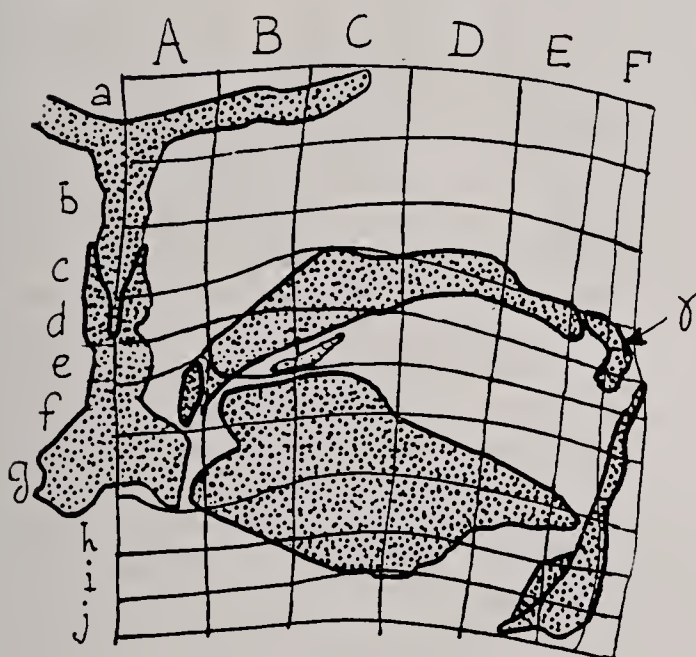
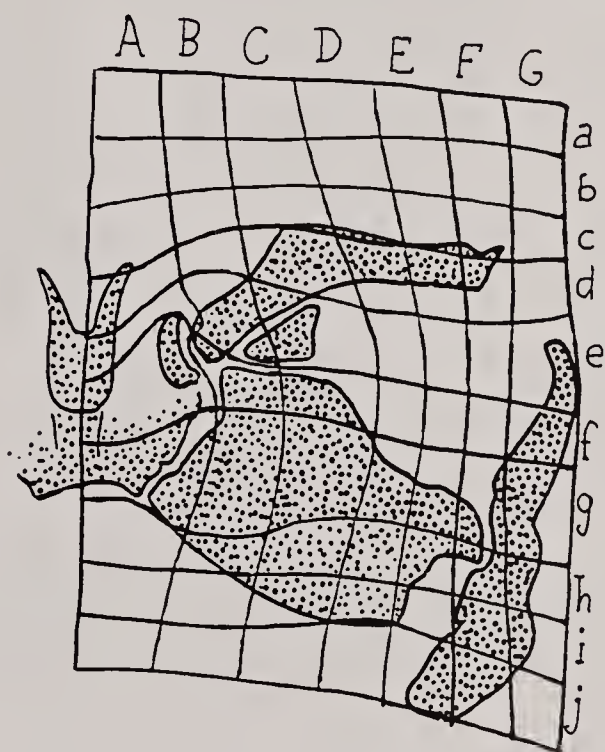
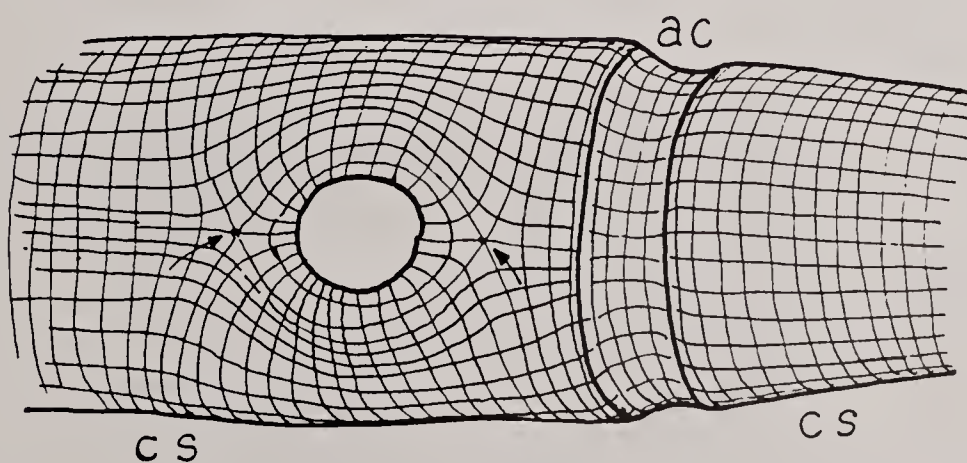
It is worth remembering that comparative studies of legs were also essential in most works on the evolution of horses, but d'Arcy Thompson did not represent the corresponding deformations, probably for the simple reason that several bones disappeared in the course of evolution, the recent horses running on limbs built from the preferential development of a unique finger. D'Arcy Thompson was aware of the limits of his theory, but he simply wrote:

> We cannot fit both beetle and cuttlefish into the same framework, however we distort it ; nor by any coordinate transformation can we turn either of them into one another or into the vertebrate type.»

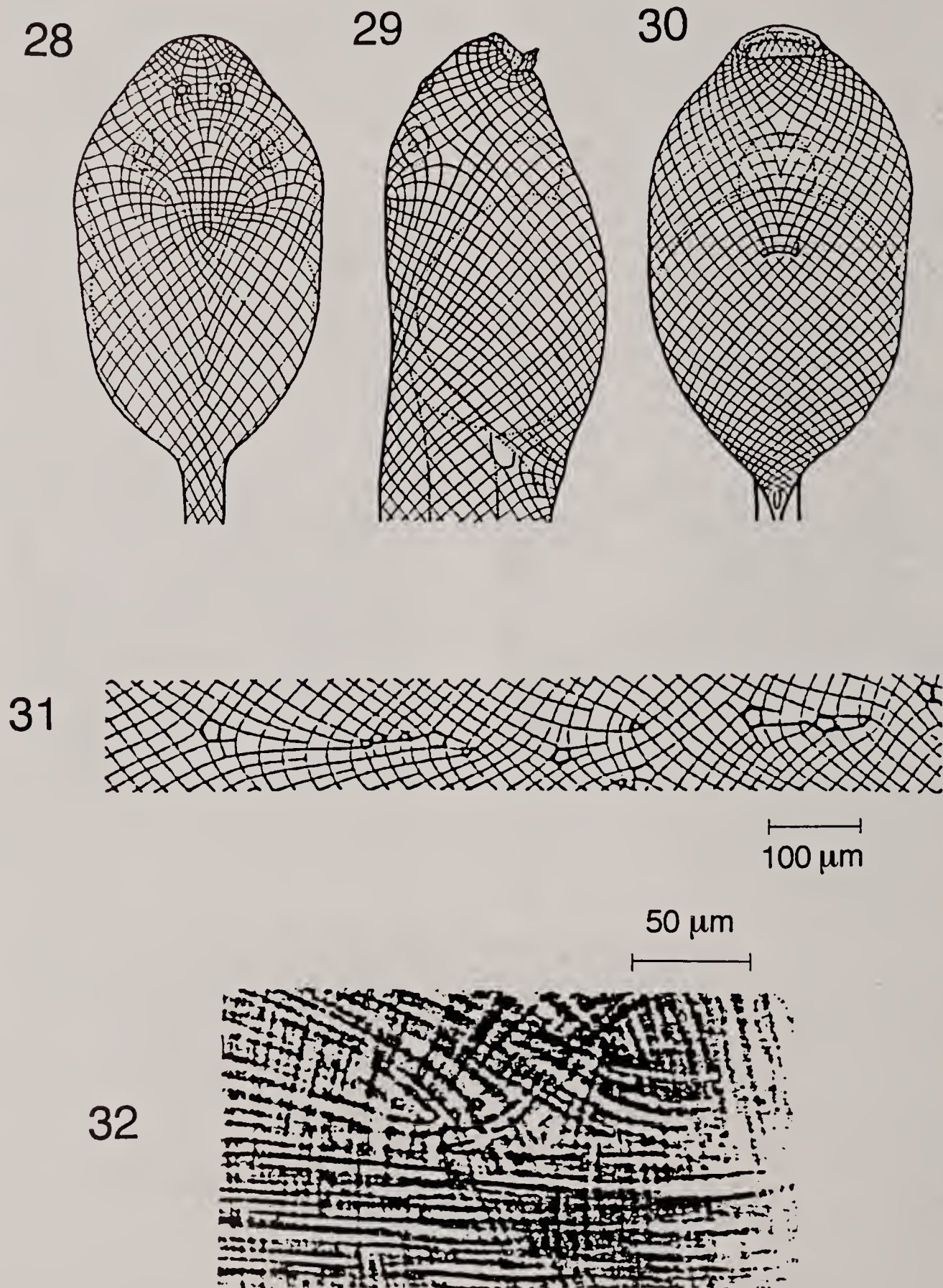
Actually this problem is still present within the vertebrate groups, studied by d'Arcy Thompson himself, and in small families such as Lamippids, the above-mentioned parasitic Copepods. Singularities seem to be necessary in transformation grids and this indicates that extreme continuous deformations invented to fit any shape in the same framework are very suspect and the main danger is the blind application of computer programs created for that. It is probable that many accurate morphologists, among zoologists, botanists and paleontologists tried the d'Arcy Thompson method in its original form, but abandoned it. What is surprising is the general absence of comments, in several recent papers, on the difficulties inherent to this method.

Natural grids and their singularities

More or less orthogonal arrays of fibrils often exist in the skin of vertebrates and invertebrates. The two main directions of these arrays generally lie at about 45° from the long axis of the animals. In worms such as nematods, these fibrils (mainly collagen) generally form two families of helices, either left-handed or right-handed. The skin is cylindrical and, within its thickness, layers of left-handed helically wrapped fibrils alternate with layers of right-handed ones. Such cross-ply systems exist in the integument of most annelids and in several groups of vertebrates, mainly in embryoes. Collagen is replaced by chitin in arthropod cuticles, but fibrils often form similar networks, with two preferred orientations which also stabilize at about ± 45° from the long axis of the body.

For all these animals, the preferential orientations of the fibrous lattice of the integument can be represented in projection onto the external morphology and this can be considered as a possible materialization of the coordinates framework of d'Arcy Thompson. Since, it is convenient to keep longitudinal and transverse coordinates in the body and its appendages (and for several simple geometrical reasons), it is better to consider that the curvilinear d'Arcy Thompson framework is possibly obtained with the set of lines tangent to the two normal bisectors of these fibril orientations.

Figs. 23-27 - 23-26) D'Arcy Thompson's transformations methods applied to a set of sclerites observed in the first thoracic appendages of four different species of *Lamippe*. 23) *Lamippe rubicunda*, the sclerite named j is absent in Fig. 26 (*Lamippe faurei*), whereas the one called γ seems to be absent from figures 24 and 26 (*L. aciculifera* and *L. faurei*). Sclerites α and β are particular to *L. aciculifera* (fig. 24); 27) Schematic view of an articulation in a crustacean appendage, with two successive cylindrical (or conical) sclerites (c.s.) and an arthrodial cuticle (a.c.). The lateral insertion of a bristle (not represented itself) generates singularities indicated by two arrows.

In the case of nematods, with a regularly cylindrical body, the fibrous network is formed by two families of helices of equal pitch, which are right-handed and left-handed and intersect at a constant angle (réf. in Picken). In general, animal shapes are less simple than cylindrical and fibrils form singular arrangements. This had been observed in the dermis of selacians, by Garrault (1937) and in tadpole embryoes by Rosin (1946), whose pictures are reproduced in figs. 28 to 32. More recently, a series of micrographs were obtained by a collaborator, L. Lepescheux (1988) in skins of Annelids and we deduced the models of figures 33 to 37.

The construction principle of these discontinuities is similar to that of singularities introduced in Lamippids, to apply the transformations method (but with different symmetries). We suggest (but have no proof...) that such singularities could be a necessary ingredient in the theory of transformations and that the direct pictures obtained from microscopic examination of the integument of several species, belonging to very different systematic groups, illustrate a general principle of morphogenesis and evolution of shape, but now the problem is to know the degree of generality of these singular arrangements of fibrils and to see how to build (if justifi-

Figs. 28-32 - Fibrillar structure of the basement membrane of the epidermis of a tadpole of *Bombinator* (after Rosin, 1946). 28) Dorsal view. 29) Lateral view. 30) Ventral view. 31) Series of trigonal and pentagonal singularities in the differentiation area of the gills. 32) Micrograph of a pair of singularities, with a trigonal symmetry on the left and a pentagonal one on the right.

able) maps of the distribution of these singularities at different ages.

Some of these singularities show well defined positions with respect to the anatomy, as can be seen (fig. 28-30). Other singularities have a more random distribution, and this seems to be the case for those observed in the gill region of tadpoles (fig. 31). These types of distributions are similar to those of small organs in most living beings.

Orthotaxy, plethotaxy and cosmiotaxy

Certain organs can be homologized and be given a name, on the basis of having a particular position in a linear series, for instance, as it is the case for teeth in mammals. Such organs were said to be *orthotaxic* by Grandjean (1948) and are in constant number, or say that number variations are rare. On the contrary, undistinguishable organs such as hairs cannot be homologized, one by one, and their number show strong variations between individuals. They are said to be *plethotaxic.* There is a third situation called *cosmiotaxy*, corresponding to identical organs, ordered into regular two-dimensional arrays, such as cilia in Ciliata (Protozoa) or in mussel gills, ommatidia in compound eyes in arthropods, or fish-scales. In that case also, there are strong variations in the total number of organs of this type. One-dimensional series of identical (or almost identical) organs also exist and well known examples are vertebrae in many fishes and in snakes. This situation is similar to that of cosmiotaxy, with variations of the total number of elements. (All Grandjean's references will be found in Travé and Vachon, 1975; his complete acarological works were republished from 1972 to 1975; a selection of references is proposed in Bouligand, 1989).

Singularities present in the natural grids of the integument in various animals are either orthotaxic, plethotaxic or cosmiotaxic, and therefore present a common character with small organs such as bristles and other formations of the integument. We find essential the fact that certain singularities of the natural grids in the integument can be homologized as other organs can be (teeth and bones in mammals, bristles and sclerites in arthropods). This fact is quite natural since the presence of small organs as bristles imply the presence of singularities in the fibrous grid of the skin. But certain singularities exist without the differentiation of associated organs.

Remarks on d'Arcy Thompsons's position relative to Darwin's theory

D'Arcy Thompson's methods of continuous transformations represent a strong support to the gradualist views of Darwin (*Natura non facit saltum),* but since their author himself observed some limits to his theory, this was interpreted as an opposition. D'Arcy Thompson is often considered as non-Darwinian (Edelman, 1992). Bookstein (1977) indicates that «the sturdy popularity of d'Arcy Thompson's book resides rather in its own unique method, a quite non-Darwinian search for geometric simplicity...» The facts are that Darwin wrote a preface for the first published book by d'Arcy Thompson, a translation of H. Müller's *Fertilization of Flowers* and, much later on, d'Arcy Thompson was Darwin medalist of the Royal Society. The fact is also that d'Arcy Thompson felt unsatisfied with some points of Darwin's theory, but I suppose just as Darwin himself was about many of his own conceptions. D'Arcy Thompson defines himself very clearly his position, when he writes:

> «It would, I dare say, be an exaggeration to see in every bone nothing more than a resultant of immediate and direct physical or mechanical conditions, for to do so would be to deny the existence in this connection, of a principle of heredity... I maintain that it is no less an exaggeration if we tend to neglect these direct physical and mechanical modes of causation altogether and to see in the characters of a bone merely the results of variations and of heredity.»

In his book *On growth and Form,* d'Arcy Thompson presented a highly documented study, which can be considered (it is my opinion) as a contribution to Darwin's theory, even if d'Arcy Thompson discussed some paragraphs or sentences from *the Origin of Species.* An interesting example corresponds to the following question asked by Darwin:

> «There is no obvious reason why, for instance, the wing of a bat, or the fin of a porpoise, should not have been sketched out with all the parts in proper proportion, as soon as any structure became visible in the embryo.»

D'Arcy Thompson indicated that a plausible answer comes from what we call today *dimensional analysis* and scale constraints. An engine which works perfectly at a given scale does not do so at a different one, because laws governing mechanisms are not invariant with dimension and, as pointed out by Galileo more than three hundred year ago, this also applies to nature and living systems.

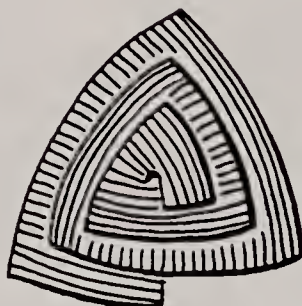
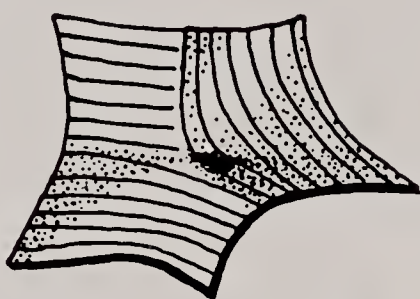
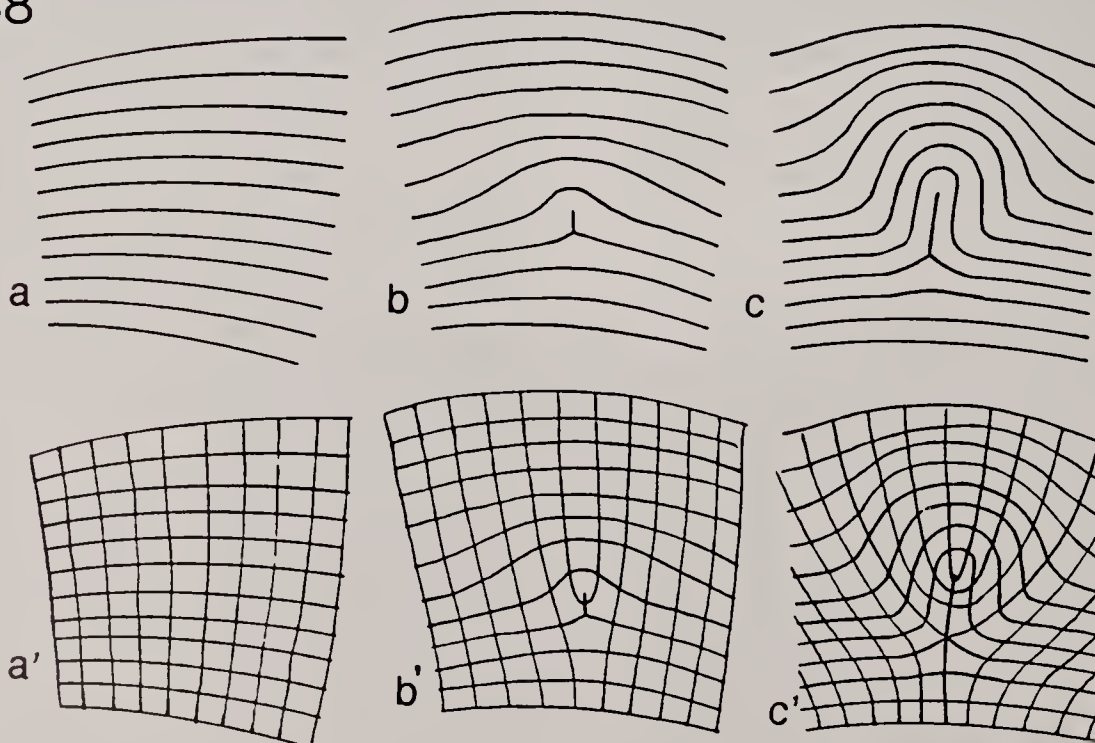
The very point which differentiates d'Arcy Thompson from Darwin is the question of discontinuities and this is clearly presented in the last lines of his book entitled *On Growth and Form*:

> «In short, nature proceeds *from one type to another* among organic as well as inorganic forms; and these types vary according to their own parameters, and are defined by physico- mathematical conditions of possibility. In natural history Cuvier's types may not be perfectly chosen nor numerous enough, but *types* they are; and to seek for stepping-stones across the gaps is to seek in vain, for ever.
>
> This is no argument against the theory of evolutionary descent. It merely states that formal resemblance, which we depend on as our trusty guide to the affinity of animals within certain bounds or grades of kinship or propinquity, ceases in certain other cases to serve us, because under certain circumstances it ceases to exist. Our geometrical analogies weigh heavily against Darwin's conception of endless small continuous variation; they help to show that discontinuous variations are a natural thing, that *mutations* -or sudden changes, greater or less- are bound to have taken place and new *type* to have arisen, now and then. Our argument indicates, if it does not prove, that such mutations, occuring on a comparatively few definite lines, or plain alternative, of physico-mathematical possibility, are likely to repeat themselves: that the higher protozoa, for instance, may have sprung not from or through one another, but severally from the simpler forms; or that the worm-type, to take another example, may have come into being again and again.»

These two last paragraphs give probably the reason why d'Arcy Thompson is sometimes classified as non-Darwinian. The opposition appears between considerations which actually are two conjectures: the one proposed by Darwin that any complex organ has been formed by numerous, successive, slight modifications and the one proposed by d'Arcy Thompson, of the absence of stepping stones across the gaps between main systematic types.

Darwin knew that important and sudden morphological changes observed under domestication or under natural conditions did not resist natural selection and that fertility also involved continuity, at a

level which will be called, in modern terms, genomic compatibility, what corresponds to only small differences between allelic genes.

I am less tempted to follow d'Arcy Thompson in his conjecture for several reasons. The introduction of discontinuities in a curvilinear coordinates framework, such as those considered above and represented on figures, can increase considerably the bearing of the method. Pairs of singularities can be generated continuously (this is mainly a matter of definition) and this is illustrated in fig. 39. In a certain way, this continuous birth of discontinuities is analogous to speciation which also can be a continuous process, even if the result is a discontinuity: the existence of well separated species. Now, it remains difficult to know the extent of the transformations theory, rehandled with such topological changes. It is probably a new tool to compare the main types of vertebrates. The question as to whether this principle affords continuous solutions to pass for instance from a beetle to a cuttlefish is far from being tackled but, even extreme, such transformations cannot be excluded.

Figs. 33-38 - Various singularities were observed by L. Lepescheux in Annelid cuticles. Instead of being interwoven, as admitted by Rosin, fibrils form separated and superimposed sheets, even in the very neighbourhood of these singularities. 36 and 37) These patterns are associated with shapes which are not applicable onto a plane (saddle point and bump). 38) Semicontinuous formation of a pair of singularities in a set of aligned fibrils (a, b, c). Correlative differentiation of a pair of singularities in a d'Arcy Thompson's grid.

Liquid crystals and the origin of natural coordinate grids

Biological analogues of liquid crystals

I have shown in several works (see ref. in Bouligand, 1978) that the organic matrix of skeletal tissues often presents a continuous structure which is that of a particular helicoidal liquid crystal, but is stabilized by several types of chemical cross-links. There are many examples of these non fluid analogues of liquid crystals in biological systems. Liquid crystalline self-assembly of collagen was obtained recently by Giraud-Guille (1992) and works on similar processes with cellulose and chitin are in progress at McGill University, with Revol *et al.* (1992, 1993). I studied the singularities of these liquid crystals and of their stabilized forms, mainly in the crab exoskeleton. The structure of these singularities is accessible, but the real problem is that of their distribution relative to the anatomy and to the external morphology.

Grids in the integument of worms, insects and amphibian tadpoles, mentioned above, come from the stabilization of liquid crystalline secretions (collagen or chitin), with preferred orientations due to various mechanical constraints under the control of cells. There are examples of parallelism between cytoskeletal elements and just secreted extracellular fibrils, when they adopt certain preferential orientations, different from those followed in pure self-assembly processes (ref. in Bouligand and Giraud-Guille, 1985). This has been observed in fish-scales and in plant cell walls. We suppose that similar relations between epidermal cytoskeleton and extracellular matrices exist in the insect cuticles and in the vertebrate compact bone. Many cross-ply structures appear under these conditions and continuous passages are often observed from purely helicoidal systems, which are analogues of liquid crystals, to these cross-ply systems, with preferential orientations.

Singularities in liquid crystals and in their biological analogues

The distribution of molecular orientations in liquid crystal varies continuously and is often represented by vector fields. It follows that singularities in such systems resemble those usually considered in vector fields, but very different types of singularities are also observed. The spontaneous arrangements of molecules around these discontinuities lead to a rich world of morphologies and similar organizations exist in biological analogues of liquid crystals (ref. in Bouligand, 1981).

It is well known that one of the parameters governing crystal growth, is the density of these very special singular lines named screw-dislocations. These dislocations are involved in the growth of enamel apatite crystals and that of the nacre in molluscan shells, for instance. The screw character is also present in singularities considered above, observed in different skin networks whose structure recall the d'Arcy Thompson curvilinear grids. Similarly, liquid crystals show various lines of discontinuity, called dislocations, focal lines and disclinations, which also play important rôles in the assembly and in the general morphology of these phases. These singularities can be observed directly in stabilized tissular structures, such as the arthropod cuticle for instance, which differentiate by liquid crystalline self-assembly. On the contrary, in compact bone, such singular lines probably exist, but are extremely difficult to recognize and to identify in the microscope. The problem of their distribution is beyond me in this material, but indirect methods could be considered.

The problem is to study, in liquid crystals and in their biological counterparts, the deformations introduced by a given density of singularities, when these latter are easily observed (some common liquid crystals and demineralized crab cuticle for instance). This is a geometrical problem for microscopists, with no obvious answer at the present time. If some general laws can be deduced, then a new approach would be possible in the comparative studies of animal shapes, but much work is still necessary to prepare research in this field.

With the introduction of singularities in comparative morphology, we have to look to macroscopic characters corresponding to long range rearrangements of fibrils around these singularities, whose core however is generally observed at the ultrastructural level. The various topological rehandlings of tissues very often leads to such ultrastructural discontinuities, which generally lie outside of the examined surfaces or sections. These basic construction patterns come from self-assembly processes and from a series of cell activities.

Plesiomorphic ultrastructures

Difficulties with the concept of synapomorphy

Strict reversibility and parallelism are considered as unlikely, when the characters under consideration are defined with a very large amount of information and represent something as a signature of the common origin of a group of species. This comes from simple considerations on probabilities. Long series of independent events never reproduce and never give long palindromes. This leads to introduce a *parsimony principle* in the construction of cladograms. However, a strict application of this principle ignores that evolutionary events are far from being independent and there are many examples of parallelism hardly compatible with this parsimony principle (Gosliner and Ghiselin, 1984). There are many possible causes for the existence of similar characters between related species: *symplesiomorphies, synapomorphies,* different forms of *parallelism* and among them: *parallel selection influencing physiologically analogous structures,* parallel selection influencing *homologous structures,* parallelism due to common inherited factors causing incomplete synapomorphy (Saether, 1979, 1983).

In the case of the above considered parasitic copepods, we first believed that the axopodlike aciculae corresponded to a synapomorphy and de Zulueta considered this trait as essential for classification. We still think that this character is useful in the local systematics of the family of Lamippids, but we gave up the idea of a synapomorphy, when more or less related structures were discovered in some species of ascidicolous copepods. Other characters such as morphology of sclerites and distribution of bristles

showed more combinations with the presence or absence of aciculae, than those acceptable in a purely cladistic conception, with a strict application of the parsimony principle. At the present stage of knowledge, we cannot choose between two possible hypotheses: 1. The first Lamippids beared aciculae and this character was already present in the most recent ancestors common to Lamippids and these ascidicolous copepods. 2. An opposite hypothesis is that expression of aciculae is a threshhold dependent character, which appears at preferential sites (furca, bristles) and sometimes on the whole surface of the parasite, if there is a large overstepping of the threshold.

This leads us to admit that certain characters are less rare than we can think at first and could be latent, waiting for a propitious situation, genetic or not, to be expressed. Then, what we believed to be a local synapomorphy transforms into a symplesiomorphy defined by a character shared by a large group of species, at the genotype level for instance, but not necessarily at the phenotypic level. Some groups of species are able to express the character in the systematic group, but this character does not justify a cladistic regrouping. Let us call this situation an *underlying symplesiomorphy*. This situation is very close to that called *underlying synapomorphy* by Saether (1979), since the considered characters concern a narrow group. Here we prefer to speak of underlying symplesiomorphy, because we consider the expression of genes common to a much larger group than the examined family. Such underlying symplesiomorphies are known experimentally, since many insects have two pairs of wings, whereas flies have only one, the posterior pair being replaced by small «halteres». We learnt, some years ago, that some genetic experiments suffice to restore the expression of a normal pair of posterior wings. We want to suggest that this situation also exists naturally in very large systematic groups, well defined by certain constant characteristics, whereas other traits are expressed here and there in the group, but are probably more constant in the genotype.

Expressed symplesiomorphies

The group of *Spiralia* (Annelids, Molluscs, Rotatorians, some Platyhelminths, etc.) is defined by the oblique orientations of the first cell cleavages in the egg. Another character which is rarely taught is that most *muscles are obliquely striated,* the distribution of myofibrils leading then to *helical* or to *double-oblique* patterns (figs. 40-42). This character seems to be constant and is observed in all Annelids, Molluscs, Rotatorians, flat and round worms, Bryozoa, Brachiopods, etc. There are however examples of perpendicularly cross-striated muscles in Molluscs and Annelids, for instance in the fast portion of the adductor of the scallop and also in the proboscis of certain Polychaetes (Annelids), but in all these animals most muscles are obliquely striated or smooth (ref. in Bouligand, 1966c). Obliquely striated muscles are absent in all other groups (Coelenterates, Echinoderms, Tunicates, Vertebrates). The oblique striation of at least a part of muscles seems to be an excellent example of plesiomorphy for the Spiralia *sensu lato* (and an excellent synapomorphy, when Spiralia are compared to the other groups). There is also a special kind of myosin, the main protein of thick filaments in muscles, which is also a good characteristic of the whole group of *Spiralia.*

Underlying symplesiomorphies

We shall now consider another character of *Spiralia*, which seems to be general, but not always expressed. Two groups of Annelids (Polychaetes and Oligochaetes) are defined by several characters, an essential one being the presence of bristles regularly distributed along metameres. These bristles show very constant ultrastructures in thin section (fig. 43).

Each bristle is produced in a follicle, which is a finger-like invagination of the epidermis. A highly differentiated cell, present at the bottom of the invagination, is called chaetoblast, since it seems at first view responsible of secretion of the whole bristle, made of chitin principally and some associated proteins. The secretion occurs at the basis of a set of parallel microvilli, which control the bristle formation, which proceeds by pure accretion at this level. New microvilli are differentiated, whereas others are dedifferentiated in the course of the secretion, whose intensity also varies and can be stronger between certain microvilli; this produces bending and other morphological characters of bristles, used in the recognition of species. Some lateral cells of the follicle are also involved in the secretion process, by adding new materials, possibly by intussusception, or simply by external accretion (Bouligand, 1967). Phenolic tanning also comes from this lateral contribution (Lehy, 1966).

Structures closely related to Polychaetes bristles were observed over the mantle surface of some cephalopods: Kölliker organs of the hatching Octopus (Brocco et al., 1974), in some Brachiopods, Lingula for instance Storsch and Welsch (1972), cylindrical spicules in Chitons (Prenant, 1923), in Pogonophora (Gupta and Little, 1970) etc. In all these examples, as in Polychaetes, also in Oligochaetes and Echiurida, the secretion of each bristle is guided by one cell differentiated with microvilli: the chaetoblast, and there are lateral productions due to follicular cells. These very characteristic structures are generally absent in molluscs, but reappear in certain genera, such as *Octopus* in Cephalopods and *Chiton* among Placophora, with various distributions and at precise stages in the life cycle.

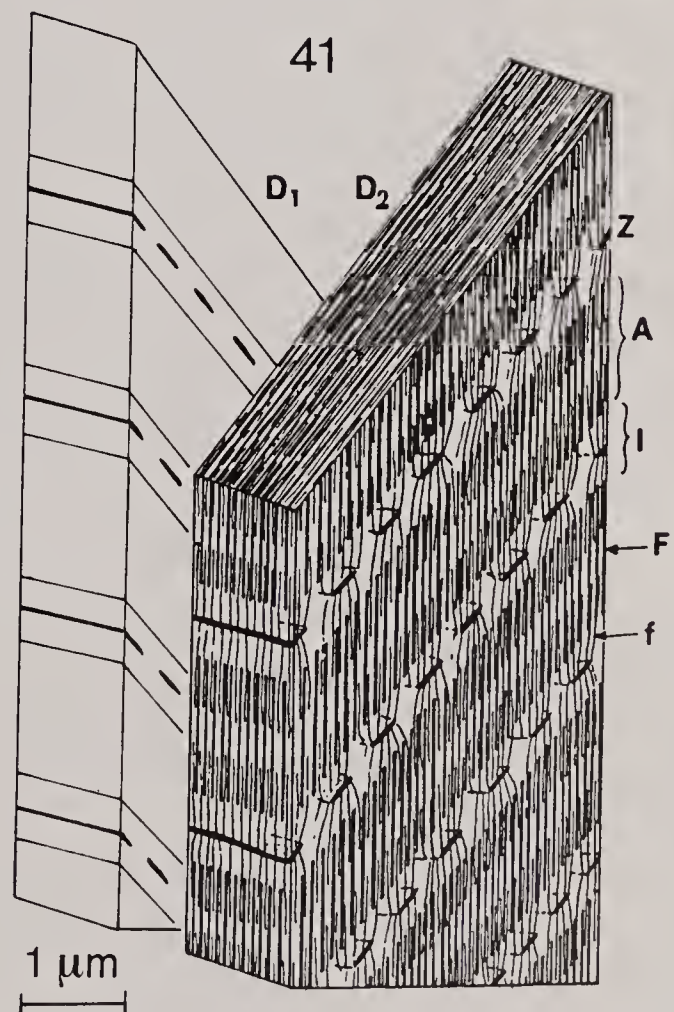
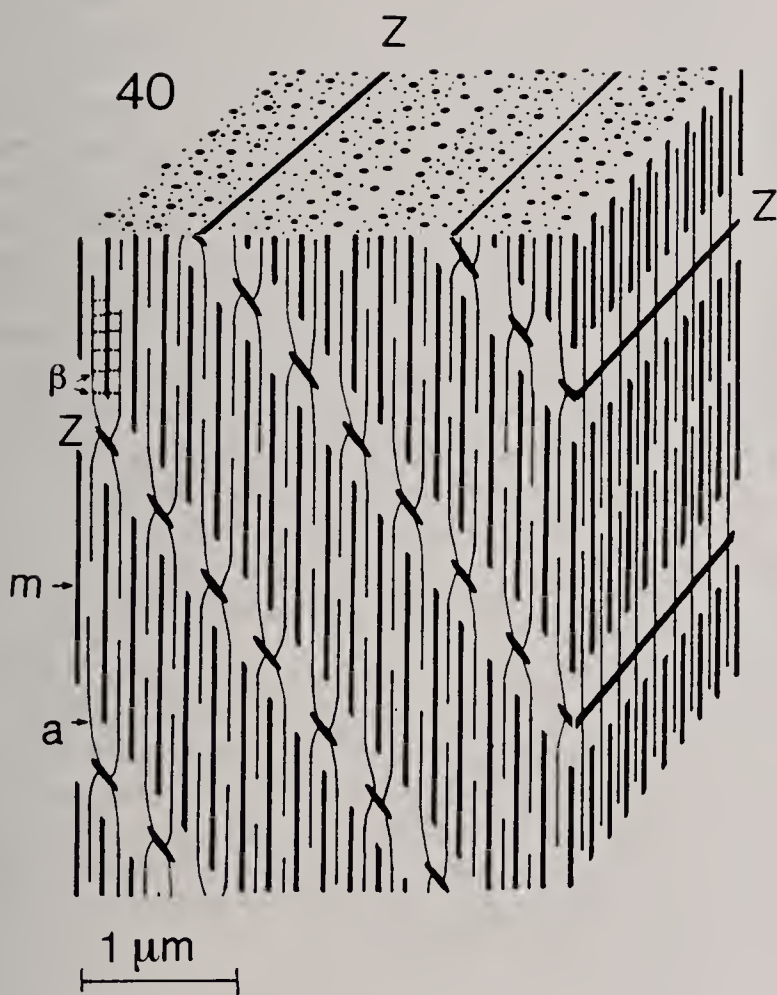
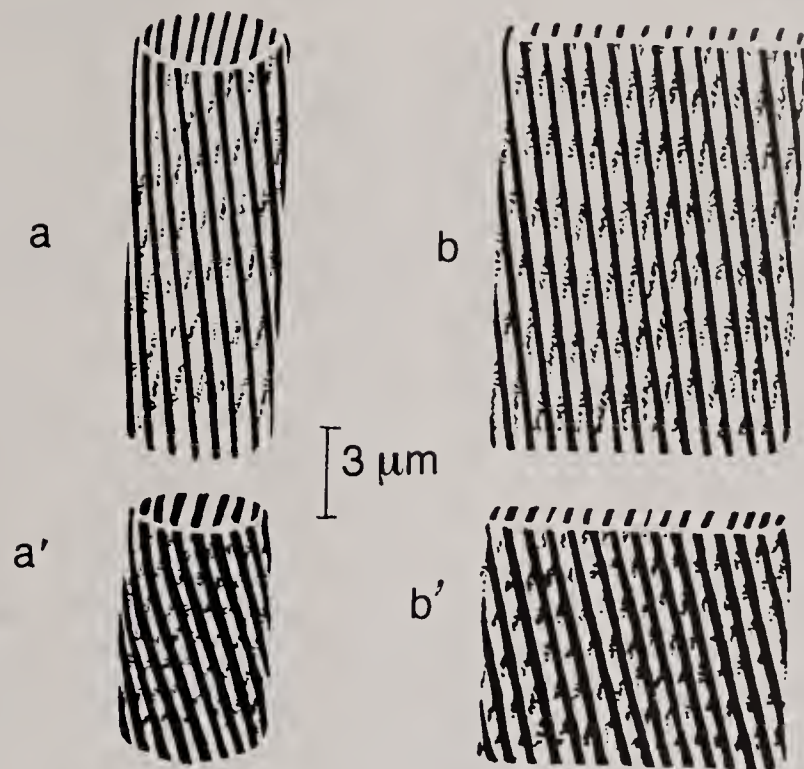
Aciculae of Lamippids, the parasitic copepods considered above, are very different from these bristles observed in several groups of Spiralia, since their structure is rather analogous to that of axopods in Actinopoda. However, the distribution principle of this type of organ seems to be similar. Copepod aciculae are generally absent, but when expressed, they are gathered at the extremity of non-sclerified bristles, and, in certain cases they appear on the whole surface of the body. In the case of Spiralia, when bristles are expressed, they are either concentrated in parapods (Polychaetes), but they can cover a large area of the body within the egg, before hatching, in certain cephalopods. Such resurgences of a character hidden in the genome are plausible, but have never been fully demonstrated to occur in natural conditions. The confirmation of such a hypothesis could represent a severe difficulty in the application of cladistic methods. The problem in this method is to re-

Figs. 39-41 - 39) General aspect in the photonic microscope of the contracile apparatus of helically or double-obliquely striated muscles in Spiralia (mainly Annelids, Molluscs, but also in flat and round worms. Brachiopods, Bryozoa, Vestimentifera, etc); a and b: relaxed state; a' and b': contracted state.

Fig. 40 - General ultrastructure of obliquely striated myofibrils (Z: Opaque element to which are attached thin actin filaments a; m: thick paramyosin filaments interdigitated with thin actin filaments; β: cross-bridges linking thick and thin filaments).

Fig. 41 - The ultrastructure of this muscle is replaced in the general pattern of double striation (D_1, D_2) and according to the section plane, one gets aspects which are those observed in smooth muscles, in cross-striated muscles and in oblique-striated muscles. F and f: thick and thin myofilaments; A: zone of interdigitated thick and thin filaments; I: zone with Z elements and attached thin filaments.

cognize, when a character presents two different states, which one is primitive and which one is derived. Another question is simply to have a clear definition of the two states of a unique character.

The difficult determination of the time arrow in phylogeny

Geologists were the first to recognize situations in sediments and in rocks, clearly indicating for two events from a remote past which one preceded the other one. Developmental biologists have a direct evidence of the embryo transformations and of their order in time. On the contrary, evolutionary biologists are faced to numerous problems to get such evidence about the time arrow.

The available criterions

The agreement between scientists in evolutionary biology comes mainly from the connected character of the trees they build. These minimal graphs reproduce the genealogies of species with more or less accuracy, and the knowledge of the time arrow at one point of the tree often suffice to orientate a large part of it. The problem is however to build these minimal graphs and to find some good examples which allow one to recognise which characters are ancient and which ones are new.

The available information on the arrow of time in evolution comes from paleontology and from considerations about complexity and differentiation. The concept of molecular clock, even with its inherent difficulties, can be very useful. Comparisons between ontogeny and phylogeny are not always accepted, but in this domain the concept of organ priority and its measurement, introduced by Grandjean (1942) is useful and is related to hierarchies observed between embryonic inductions and between the expression of genes involved in development (Bouligand, 1989). This is a to wide problem to be considered here.

Regression and multiplication

There is another type of criterion observed by Grandjean, from his studies on phylogeny and ontogeny of mites, mainly the Oribatids and he deduced certain rules. One of them concerns the arrangement of small organs like bristles in the external morphology. The evolution leads to a progressive *numerical regression in one or several series of orthotaxic organs,* which can be followed, more or less suddenly, by a *multiplication* of these small organs, presenting then an *anorthotaxic* situation (pletho-or cosmiotaxy). Similar evolutions are plausible in different lineages of Vertebrates: the number of vertebrae was reduced, certain vertebrae being progressively specialized, in many Amphibians and Reptiles. Then, multiplications of vertebrae appeared, according to a highly uniform model, possibly in Apods, in Ophidians and in the slow-worm, *Anguis fragilis,* for instance. The situation could be similar for the teeth of Mammals, whose number was progressively reduced in several groups, whereas the differentiation between incisors, canins and molars which was reinforced, but sudden multiplications of teeth appeared in some «edentate» mammals and in Cetaceans (Odontocetes) for instance; teeth were replaced by multiple «whale-bones» in other Cetaceans, the whales (Mysticetes).

In our Copepod family, that of Lamippids considered above, the appendages in the genus *Linaresia* show the maximum reduction of bristles known in the whole family, and there is simultaneously a strong multiplication of small papillae of the integument in the same cephalothoracic region, but our study of this family is not as well documented as that of Grandjean dealing with Oribatids.

Comparison with crystals (solid or liquid)

If true, the scenario of evolution considered by Grandjean probably applies to singularities observed within natural grids of the integument of numerous species and of their embryoes. The concepts of ortho-, pletho-and cosmiotaxy can be applied to the singularities represented in Rosin drawings (figs. 28 to 31). For instance each eye presents a lateral pentagonal singularity and this corresponds to an example of orthotaxy, whereas the pentagonal and trigonal singularities, observed in the area corresponding to the future gills, are more or less randomly distributed and this corresponds to an example of plethotaxy. As quoted above, one finds in liquid crystals (and also in true crystals), various rearrangements of the network, which correspond to singularities (also called dislocations or defects), whose distribution is called *texture* (Bouligand, 1981). The texture geometry depends on conditions prevailing during crystallization and on the nature of various other constraints. In such systems, there are dislocations occupying higly «functional» positions, whereas others are more or less randomly distributed. This term «functional» can appear as exaggerated, but this is not always the case since, in true crystals, there are «screw-dislocations», whose presence accelerates the cristallization process. To come back to the living systems, these singularities exist in many tissues and constraints leading to various textures come mainly from a cell control.

Diversity and macroevolution

This work is a review of the main difficulties encountered in my own studies to connect a set of morphological data into a coherent evolutionary interpretation. One of the obvious conclusions is that *animal diversity* remains very difficult to appreciate, this being shown by the study of Lamippids, this small and apparently homogeneous family of parasitic Copepods, which however shows extreme examples of macroevolution. Recent hypotheses in paleontological literature give also an evidence of the difficulty to appreciate diversity and this deserves a discussion. There is a second conclusion, which is that, beside *heterochrony,* there is another mechanism of macroevolution, that of *heterotopy.* This term is used mainly in medical sciences and means the abnormal displacement of an organ or a tissue and seems be rare in the evolutionary context, but could mean a change in location of well identified parts of the body. If small genetic changes are able to modify the order in the ontogenic time of essential

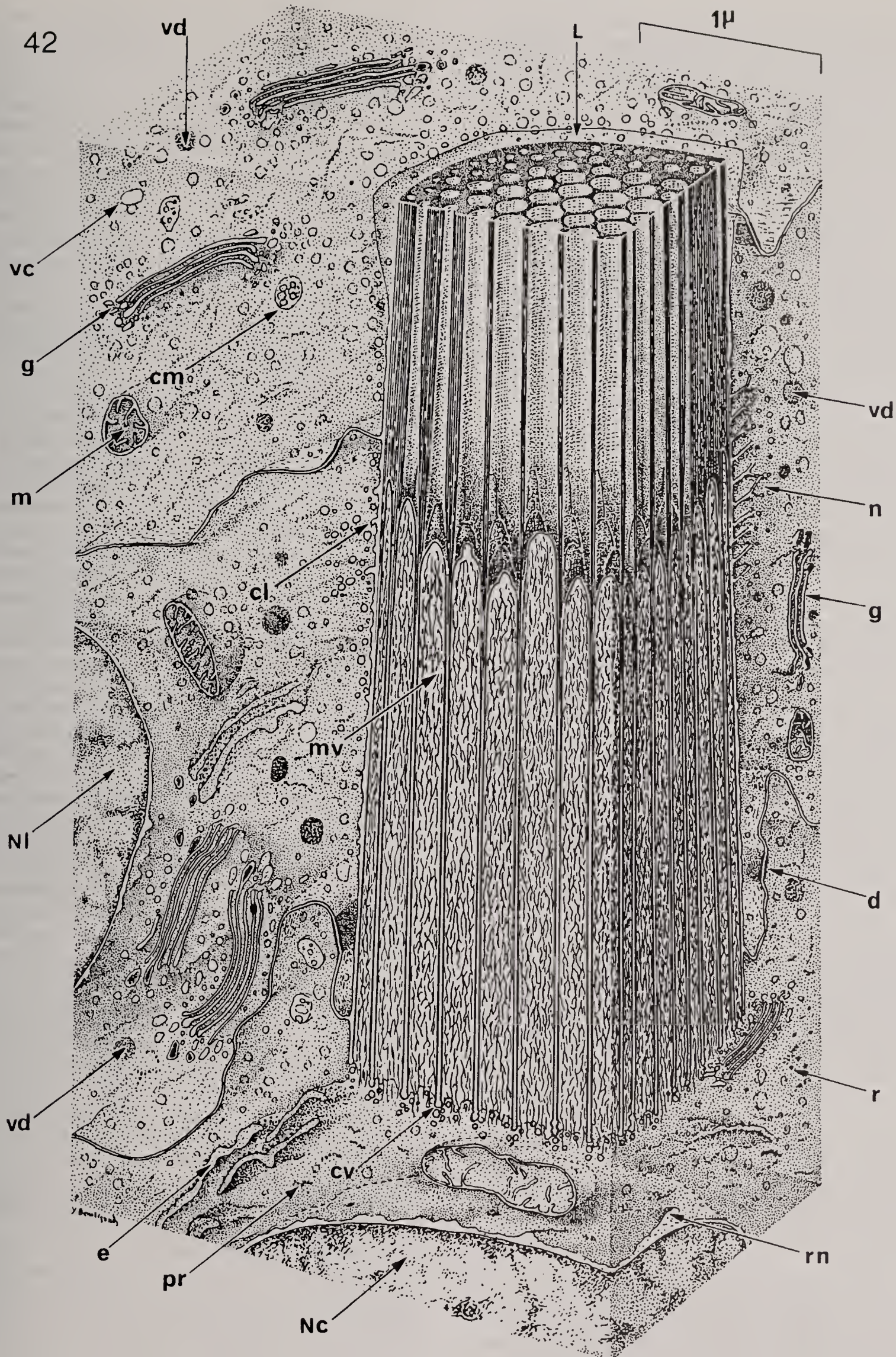



Fig. 42 - General ultrastructure of an Annelid bristle. A 90° sector of this more or less cylindrical secretion is represented; the apical region of the chetoblast, with its nucleus Nc, form a set of parallel microvilli (mv), which are a guide to chitin secretion vesicles (cv); other secretory activities are observed in lateral cells, with their nuclei (Nl) and their vesicles (cl) at the level of the tips of microvilli; these lateral secretion vesicles often form prismatic patterns (n); the two membranes of the nuclear envelope often show large separations (rn); at a distance of microvilli there is a free space (L) separating the bristle from lateral cells of the follicle; very usual cell organelles are observed: various cell junctions (d), ergastoplasm (e) Golgi apparatus (g), mitochondriae (m), polyribosomes (pr) and free ribosomes (r), various types of vesicles: (vc, vd). Bristles with similar or closely related ultrastructures are found in isolated species or in some groups of Spiralia.

developmental events, one can expect that other genetic changes can modify the domains, in the morphological space, where some characters are expressed, and also the morphology of these characters. A change in time is often correlated with a change in space and conversely. So, the idea of heterochrony suggests that its spatial counterpart, heterotopy, could be an evolutionary mechanism.

The difficulty to estimate diversity

Recent articles deal with remarkable fossils discovered ninety years ago and propose, from their restudy, that main systematic groups appeared during a relatively short geological period, the *cambrian explosion.* Despite the high quality of these fossils and some ones recently discovered, it is difficult to understand how several authors conclude that such observations demonstrate a sudden macroevolution occuring in many groups, with no equivalents in later periods. Main phyla and classes are probably very ancient, but this is established from the study of numerous fossils collected by successive generations of paleontologists and not from a particularly rich fauna discovered in some very old sedimentary formations.

The question can be reasked differently. How to estimate for instance the extreme morphological changes observed in parasitic copepods, and particularly those within this narrow family of Lamippids, and then to compare them to those considered in these cambrian organisms? These copepods possibly existed and diversified in the cambrian seas, but actually we have no accurate information. Extremely large variations also are common in many other groups of invertebrates. How to measure the amplitude of such variations in living species and to compare them to those in extinct faunas? Methods do not really exist in the present state of knowledge, but some indices are possibly available and, apparently, they are never considered in these papers.

An accurate knowledge of diversification in living beings and its chronology will come from detailed analyses of genomes and of many phenotypic characters, but this still exceeds our present capabilities, and perhaps will for a very long time. I suppose that the overestimate of diversity in a fossil fauna could be related to the fact that most zoopaleontologists work on bones and shells, which are homogeneous structures in vertebrates and molluscs. The knowledge of diversity comes more from neontological studies (zoology and botany), than from paleontology. In my opinion, the gap separating paleobotany from botany is less important than the one between paleozoology and zoology.

Heterochrony and heterotopy

Small causes produce important effects, when conditions are not far from those of an instability and this can be the origin of discontinuities appearing in a continuous context. Examples are known in irreversible thermodynamics, in phase transitions for instance, and this conception has been generalized in the frame of a topological approach of dynamical systems (Thom 1972). This is a general principle in physics, which certainly applies to many situations in biology and possibly in species evolution. This idea of continuously evolving parameters controlling a change, with more or less sudden effects, was possibly present in the mind of Schiaparelli and also Volterra (Scudo, 1991, 1994).

Simple genetic changes can modify the development rate of a given organ, and the result is a new shape of the whole body. This corresponds to heterochrony (displacement, acceleration or retardation of an ontogenetic process within the general context of development). What was considered in our examples (from copepods to vertebrates) corresponds to similar changes, possibly generated by small genetic variations, but instead of a change considered along the time axis, the relevant axes now are those of the coordinate grids, these cartesian coordinate frames which are made curvilinear, with the possible introduction of singularities.

Such topological rehandlings are obvious things for certain microrganisms: for instance, the Radiolarian skeletons showing the symmetries of the Platonic bodies, described by Haeckel (1887) in one of the Challenger Monographs. The useful pictures are reproduced in the book of d'Arcy Thompson in his fig. 340. Some ornaments show that the represented species are very closely related, but since they have the symmetries of different regular polyhedrons (octahedral, dodecahedral, icosahedral), there are no continuous passages between these phenotypes, whereas the genetic differences could be small.

A change in the number of facets in Radiolarians can be compared with another discrete variation, that of the number of fingers. This latter has generally a genetic origin, which is however much less than the differentiation of a new species. It is not excluded that some individuals among populations of such polyhedral Radiolarian show the symmetries of a different polyhedron. I do not read literature enough in this domain to know whether or not is has been observed. However, strong heterotopic variations are to be expected within this group. It appears also that the introduction of coordinate frames on such morphologies would resemble the representations of harmonic functions onto a sphere, with the corresponding singularities and polyhedral symmetries. The passage from one solution to another one is discontinuous, but could be parametrized continuously within a rather simple model.

Let us recall that regular polyhedral morphologies are very common in flower pollens and similar discrete variations occur among closely related species. Polyhedral morphologies also exist in many viruses, but passages to different symmetries are generally excluded in that case, but there is possibly a sort of exception, in certain giant T4 bacteriophages with much longer head than usual.

Topological rehandlings are regular processes in ontogeny and in phylogeny of animals and involve the introduction of singularities, whose existence is demonstrated in some materials, but much more information is necessary to introduce these concepts in the very foundations of developmental and comparative morphology. Singularities have long range effects or not. One obviously observes the intermediate situations. The importance of deformations produced by a dislocation in a crystal is called the «mass» of the defect by crystallographers. Similar parameters could be introduced in biomorphology but this seems to be to early.

Conversely, the concepts of orthotaxy, plethotaxy and cosmiotaxy, which come from biomorphology, could be introduced in crystallography, since dislocations are distributed either randomly, with a more or less constant density (plethotaxy), or form regular lattices (cosmiotaxy), form definite patterns called *textures,* where many singularities occupy definite places and can be given a name.

Grandjean observed that series of events are arrowed in the evolutionary time. Similarly, in crystals, it can be easily verified that textures present irreversible types of evolution, since *hysteresis* is a general rule in the behaviour of defects or dislocations. One can find examples in liquid crystals showing how regression in the number of singularities leads to orthotaxy. If the singularities number decreases below a certain threshold, the texture either disappears or is conserved but higly rehandled, if some parameter is changed, for instance temperature variation or introduction of an external field. Similar changes in the biological context could correspond to a strong increase in the number of cells in a given tissue. Orthotaxy is then followed by anorthotaxy. In the same line of thought, let us recall that screw-dislocations can be considered as «functional», since their rôle is recognized as essential in crystal growth.

Well known examples of topological rehandling are observed in *Drosophila*, with those processes called *transdetermination,* the mutation *Antennapedia* for instance, leading to the production of two more or less complete legs in the place of the two antennae. Such animals cannot resist natural selection. On the contrary, to pass from a polyhedral shape to another one for a Radiolarian is not an obvious handicap. When topological rehandlings of biomorphology are not incompatible with survival, there is a plausible place for a large evolutionary step. Such situations are probably rare, but not excluded, and the two positions of Darwin and d'Arcy Thompson will possibly represent the two interesting pôles of discussions in the future developments of research on macroevolution.

Conclusion

Self-assembly is a major process in the genesis of supramolecular structures in biological systems and is closely related to crystal growth. Among these morphogenetic mechanisms, generally considered as working at lower levels of organization, there is a particular self-assembly based on liquid crystalline phases, which can be stabilized into supple but morphologically defined structures. Liquid crystals show long range orders with remarkably diversified patterns. The fluidity of liquid crystalline secretions leads to regular shapes, which can be rehandled by resorption and resecretion controlled by cells. The ordered fluids form an essential interface between cells and the extracellular matrices, on which are based the main characters of morphology.

Among the patterns arising from liquid crystalline self-assembly and controlled by cell activities, there are sets of extracellular fibrils forming networks visibly related to the d'Arcy Thompson's grids, considered in the continuous shape transformations in evolution and development. These natural grids show the presence of singularities, those possibly corresponding to difficulties arising from the use of d'Arcy Thompson methods by pure continuous deformation of the coordinate network. The apparent distance between Darwin's and d'Arcy Thompson's conceptions about continuity comes possibly from the need to introduce these singularities, but we indicated that their introduction within a regular lattice can intervene by creation of singularities pairs, which can be considered as continuous. In physics, there are transitions which are first order, second order, and finally very soft. The creation of this kind of singularities can be considered as a very soft process...

The problem is that our personal exploration of some biological species and of liquid crystals, biological and non-biological, does not suffice to really propose general principles, since much remains to be done in the examination of singularities in cells and tissues, simply at a purely methodological level, and results in this field will need to be replaced in the context of molecular genetics, to be somewhat consistent in the studies on macroevolution.

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The Precambrian fossil record: new insight of life

Abstract – The study of the Precambrian fossil record, especially active in the second half of 20th century, reveals the phenomena that could not be predicted on the basis of the Phanerozoic experience of the classical palaeontology. Among major revelations there are astounding antiquity of life, domination of microscopic, in particular, prokaryotic organisms during the most part of Earth history, crucial role of the biota in the steady but radical change of the global environment, dramatic restructuring of the global ecosystem during the late Neoproterozoic accompanied by the rise of the eukaryotic trophic pyramid and very late appearance of the metazoans.

According to historians of science, about 2.000 species of fossils plants and 25.000 species of extinct animals had been described by 1850, i.e. nine years before the first edition of Darwin's «Origin of Species» was published. Practically all fossil species that had been described were from Europe.

Recently about a quarter of a million of the fossil species have been described from all the continents. More than 99 per cent of the fossil taxa have been described from the Phanerozoic.

Paleontology dealing with long period of time has revealed phenomena which are impossible to observe directly. Human life, and even historical time are too short to allow us to notice and to recognise slow and steady trends in the biosphere masked by numerous reversible fluctuations. That is why the ideas of cyclic, static and linear time of the world have been equally competing through the whole history of human culture (Grunbaum, 1969). Actually we do not have actualistic methodological instruments that would allow us to see difference between the long-term events and fluctuations if their duration exceeds human historical experience.

The fossil record, being the integrative result of long term processes and fluctuations, decreases the noise from the latter and, otherwise, represents more prominently the long and irreversible trends and events. That is why it was paleontology which gave the fourth dimension, namely the Time Arrow, to the recent model of Nature. The idea of biological evolution was the most fundamental and valuable discovery of classical paleontology. Evolutionary approach has subsequently spread through most other areas of the natural sciences.

The introduction of the radiometric dating of rocks has revealed the great age of our planet, i.e. 4.5-5.0 billion years against 4-5 thousand years what was generally believed according to the Christian tradition (interpretation of Bible) and even against the 100 million years, an estimation based on the comparison of the amount of salt in the world ocean and annual input of salt by rivers (Burchfield, 1990).

Radiometric dating, first invented early in the 20th century by Bertram Boltwood, a Yale physicist, has led not only to the discovery of the great age of Earth but also to the fact that the Phanerozoic makes about 1/9 of geologic history in its entirety. This fact meant that almost two centuries of classical paleontology were devoted to the study of a rather small portion of the history of life. And even though the Phanerozoic is the best documented part of life history, it is still the tail of the whole story.

Generations of geologists and paleontologists considered the Pre-Phanerozoic rocks as being non-fossiliferous. For example, the whole sequence of the Riphean sedimentary rocks accumulated between 1.6 and 0.6 billion years ago and exposed in the Ural Mountains in Russia for many years was referred to as «ancient dumb formations» because these rocks seemed to be «mute» in respect of life. Apparent absence of fossils in the Precambrian rocks was the reason for the name Cryptozoic (from Greek «cryptos» that means concealed, covert, unrevealed) for the greatest (about 85%) and the early portion of the history of life.

The Precambrian fossil record became the subject of intensive study relatively late in comparison with the age of paleontology as a special scientific discipline, i.e. effectively after 1960 although the pioneer works can be traced far back to the beginning of the century. Before the middle of our century the term «paleontology of the Precambrian» sounded strange and even later this term was rejected by some paleontologists on the grounds that many objects in the Precambrian fossil record have uncertain nature while others, for instance stromatolites, are in fact remnants of peculiar geobiocoenoses and not the fossil remains of the organism. Nevertheless during a few last decades a series of the fundamental discoveries has been made in the Precambrian fossil record, which dramatically changed our understanding of life's history and life as a phenomenon of a longer time retrospective.

It was P. S. Laplace (1749-1827) who noticed that an appeal to the vast extent of time and space gives the possibility for discovering new classes of phenomena. His statment has found a brilliant confirmation in the whole experience of classical Phanerozoic paleontology.

An appeal to the far longer history of the Precambrian life has led to the discovery of new facts of critical importance, and actually to new insights about life. It turned out that the Phanerozoic experience of

paleontology doses not exhaust the whole diversity of biohistorical phenomena. However, on the way down to the Precambrian fossil record paleontologists have met many methodological problems connected partially with the phenomena which do not have actualistic or Phanerozoic counterparts and with situations which do not allow one to use the uniformitarian approach. In a sense, during most of the Precambrian geological history the Earth was quite a different and «unfamiliar» planet. All these problems have affected the systematics of the paleontological objects as well.

One of the usuall difficulties of the Precambrian paleontology is an identification of the true biological or biogenic objects from what is called «pseudofossils» i.e. the non-biogenic objects of uncertain nature morphologically resembling fossil or living organisms. One should note that the question of how to distinguish the living objects from the nonliving ones on the basis of purely morphological characters is not quite trivial even for some recent forms (like some viruses or bacteria, especially in a latent phase of life activity). But this problem becomes really difficult in many cases of paleontological practice in particular when the specialists deal with objects of a simple morphology which can be observed in the non-biogenic objects as well (Thompson, 1942).

The matter is that in addition to the pure morphological characters which can be used as the criteria for identification of the live object, recent organisms demonstrate an ability for locomotion, growth, reproduction, metabolic activity, etc., i.e. the characters which are impossible to observe or to judge in dealing with the fossil organisms. The concept of biogenecity is poorly developed for fossil objects. Purely morphological criteria turned out to be inadequate for systematics both at the low taxonomic level and at the level of higher taxonomic categories (including life itself if one should consider it as a taxon) in the oldest part of the Precambrian fossil record. That is why along with the morphological criteria based on the similarity of problematic fossils with living or known extinct organisms one should take into account the taphonomic spectrum of the fossils as well as the mineral, organic, molecular or isotopic traces of life activity, probable place in a biohistorical or evolutionary sequence, chronological probability, position in the paleoecosystem etc. (Hofmann, 1972; Sokolov and Fedonkin, 1988).

The study of the Precambrian fossil record is connected with some other peculiarities in addition to the very long time intervals and uncertain nature of many fossil objects mentioned above.

First of all, the biotic diversity of the Precambrian fossil record looks very low if compared with the Phanerozoic one. Precambrian fossils have been collected from more than 3.000 localities all over the world, but slightly more than 1.300 fossil taxa at the genus level have been described up to now (Hofmann, 1988). Some critically inclined paleontologists evaluate the number of the «real» taxa in the Precambrian as somewhere between 500 and 900. Chronologically and stratigraphically the distribution of the Precambrian fossil localities is very uneven. About 1-5 localities per every 100 million years are usual for the Early Proterozoic, and about 10-25 localities per every 100 million years of geological history are typical for the Late Proterozoic. The Archean fossil record looks far more poor. For example, slightly more than 20 localities of stromatolites are known from the whole Archean. Thus the number of the sites where the fossils could be preserved decreases with the growing age of the rocks.

Another circumstance is that macroscopic organisms appeared relatively late and even among those microfossils which represent the procaryotic world the paleontologists identify just the large bacterial cells, in particular the cyanobacteria, while the most of other groups of the procaryotes do not yet have a fossil record because of their very small cell size (for instance, the whole Kingdom Archaeobacteria).

In spite of an exponential growth of paleobiological information from the Precambrian we still meet some serious difficulties in identifying the whole range of biological phenomena known from the Phanerozoic fossil record. There are a few reasons for this: 1) poor morphological characters and uncertain nature of many fossil groups; imperfect classification especially among the procaryotes where pure morphological characters have very low taxonomic value; 2) low biological diversity at the species level, which is the most effective for the purpose of detailed biostratigraphy and evolutionary modeling; 3) lack of data on the evolutionary lineages for the most of the Precambrian groups of organisms; 4) low precision of the biostratigraphic division and telecorrelation of the Precambrian strata if compared with Phanerozoic counterparts; 5) change in time of the environmental biotic and abiotic factors which strong influence on the taphonomic processes (such as an oxygenization of the sediment, development of heterotrophy, bioturbation, the rise of the filter feeders, etc. see Fedonkin, 1985, 1987, 1992).

In contrast with the classical paleontology of the Phanerozoic the study of the Precambrian history of life is predominantly oriented to the world of the procaryotes which dominated in the most of environments during the major portion of the history of the biosphere. The rise of the eucaryotes essentially wiped off the picture of the procaryotic world though they continue to play a great role in most biological processes. Competing with bacteria for some nutrients and habitats, forcing the procaryotes out of numerous biotopes, utilising the by-products of procaryotic life activity and consuming the bacterial biomass as food eucaryiotic organisms have changed the world and the fossil record as well.

On the other hand, in the process of the symbiotic origin of the eucaryots accompanied by the colonisation of the host cell by procaryotic organisms the latter have lost their individuality while they lost their free mode of life. So part of the procaryotes disappeared just because they became the organelles of eucaryotic cells.

And last but not least, eucaryotes have essentially contributed to the global change of environments favorable for the life activity and fossilisation of procaryotic organisms.

A great advantage of the Precambrian fossil record in spite of the difficulties mentioned above is an absence of a developed trophic pyramid above the network of procaryotic biogeochemical interactions. This circumstance opens up a unique possibility to read undisturbed paleontological, sedimentological and biogeochemical signals from the procaryotic

ecosystems of the Precambrian biosphere during most of its history. Conservatism of the procaryotes in their morphological, ecological and biochemical aspects, relative simplicity and determinate character of their biogeochemical ties and reactions make it easier to decode the geochemical and sedimentological signals of the Precambrian procaryote-dominated biota especially in the Archean and Early Proterozoic parts of the geological record.

Paleontology of the Precambrian deals with diverse microfossils, thalli of megascopic algae, metazoan body fossils and bioturbations, stromotolites and some other biosedimentary structures, biogenic minerals, kerogens, organic films, biomarkers and other organic chemofossils. Along with the pure paleobiological methods the geobiological approach (review in Fedonkin, 1993, 1994b, in press) has been actively developing during last two decades.

According to the geobiological approach the biosphere should be considered an integrated system of interacting biotic and abiotic components where life acts as the most active part of the system (Vernadski, 1926). Recent models of Precambrian climates, atmosphere and ocean chemistry, sedimentary processes, etc. do include the biota as an active factor controling those processes (Lovelock, 1979; Charlson et al., 1987; Chaloner and Cocks, 1989; Derry et al., 1992). On the other hand, the study of those processes which are usually beyond the scope of paleontology (for instance, the isotope record of carbon and sulfur) casts additional light upon the biota and environment in the Precambrian (Zavarzin, 1984; Holland, 1984, 1992; Kasting and Ackerman, 1986; Hayes et al., 1992a,b; Schopf and Klein, 1992 and references therein). The limited lenght of this paper makes me concentrate mainly on paleontological objects — on the Precambrian fossil record as it recently come to look after a few decades of intensive study.

The Precambrian fossil record demonstrates that during the major portion of the history of life the microscopic organisms, in particular procaryote, have dominated in all the habitats. Precambrian microorganisms usually are preserved a) as mummified or organic-walled microfossils, and b) as mineral pseudomorphs (silicified ones are the most common in the chert nodules or inside the silicified stromatolites and bacterial mats). Being heterogenous by their nature (eubacteria, lower eucaryotic algae, lower fungi, protozoans, cysts, eggs and egg cases etc.) the microfossils demonstrate three important trends through out the Precambrian fossil record, namely the growth of morphological diversity, increasing individual cell size and the tendency to coloniality (Schopf, 1992a,b,c).

Cell size analysis and the study of the internal structure of the microfossils were the major approaches to the problem of the nature and taxonomic diversity of the oldest Precambrian microorganisms. None of the approaches gave definite arguments. Dramatic discussions of the nature of the «dark spots» inside some of the microfossils (nucleus, collapsed protoplasm, gas vacuole or an organelle?) have led to a number of additional approaches, e.g. the study of the postmortem degradation of recent microorganisms in vivo and in vitro, experiments on the artificial fossilisation of the microorganisms, actuopaleontological and taphonomic research etc. (Golubic and Hofmann, 1976; Knoll, 1985a; Pierson, 1988; Krylov, Tikhomirova, 1988; Rothschild and Mancinelli, 1990).

These approaches were supplemented by the comparative study of the ecology of the recent bacterial communities and their Precambrian counterparts (Castenholz et al., 1992). The structure of the community and the kind of environment were supposed to give the key to the problem of the nature of the Precambrian microfossils. In particular, it was demonstrated that the recent bacterial communities of sabkhas, marshes and lagoons of the arid climatic zones might be considered as analogs for the globally dominated ecosystem through most of Precambrian life history (Awramik, 1984; Knoll, 1985b).

Later on it came to be understood that the wide range of the procaryotic tolerance and their astonishing biochemical diversity essentially exceeds the dominant environmental parameters of the recent biosphere. This observation has led to an idea that the space of biochemical diversity, the tolerance limits and the physico-chemical parameters favorable for the most intensive reproduction in some recent procaryotes may be indicative of the environments which existed on Early Archean Earth, i.e. during the periods of the rise of the procaryotic world (Knoll and Bauld, 1989).

Thus, two actualistic approaches mentioned above have given rise to non-actualistic models of the Precambrian biospheres. And again, here one can see the importance of the data on Precambrian environments for adequate paleobiological reconstructions and research on the systematics of the oldest fossils.

The most notable evidence of the microbial life activity in the Precambrian are the stromatolites. These biosedimentary structures first appear as early as 3.5 billion years ago and became widespread in Early Proterozoic as the dominant shallow water landscape of carbonate platforms. The abundance and morphological diversity of the stromatolites increased rapidly during Proterozoic and reached the maximum at about 1.0 billion years ago (Walter and Heys, 1985).

Though the stromatolites are in fact the remnants of biogeocoenoses they are referred to by Latin names to identify the formal morphological «genera» and «species» and are arranged into the formal systems according to their general shape, mode of branching, microstructure etc. The nature of the stromatolite morphological characters and of the stromatolite taxa is not well understood. However the taxonomy of stromatolites became an important instrument to search the Precambrian life history. Distinct changes in the stromatolite assemblages through the Precambrian fossil record discovered empirically by the paleontologists of the Russian biostratigraphic school (Maslov, 1960; Krylov, 1963, 1975), may reflect both intrinsic factors (such as changes in the structure and composition of the microbial communities, biological and biochemical innovations of the stromatolite-building procaryotes) and extrinsic factors (such as change in the chemistry of the ocean and the atmosphere, global climate and paleogeography, appearance of the eucaryotic groups competing with or feeding on the stromatolite bacterial communities).

Stromatolites as the globally dominating biogenic landscape of the Proterozoic shallow water environments demonstrate marked decline in their abun-

dance and diversity after 1.0 billion years ago and especially dramatic after 700 million years ago. The possible cause for the stromatolite decline might be: a) negative effect of the new evolved grazing and burrowing metazoans (Awramik, 1971; Walter and Heys, 1985); b) appearance of eucaryotic algae competing with the cyanobacteria for nutrients, habitats and light (Monty, 1974); c) major low-stands in the sea level (Gebelein, 1976); d) negative effect of the growing concentration of biogenic oxygen upon the bacterial stromatolite-building communities (Krylov, 1988); e) decreasing carbonate of the sea water during the Late Proterozoic (Grotzinger, 1990); f) climate change, in particular African Glacial Era and its paleogeographic and geochemical consequences (Semikhatov and Raaben, 1993). In fact, all these hypotheses may be complementary.

Along with the stromatolites and rare remnants of the carbonate algae which are indicative of carbonate biomineralization in the Precambrian there are other biominerals which are the mineralogical evidence of the other groups of organisms, though their cell (or body) fossils are unknown. Biomineralization is a rather usual phenomenon of life. About 60 minerals are produced by representatives of all five kingdoms of the organic world and biomineralogical diversity is far from being exhausted (Lowenstam and Weiner, 1989).

Biominerals which have a unique shape of their crystals as well as other physico-chemical properties can easily be distinguished from their abiogenic counterparts and may be used as markers of certain groups of organisms in the geological record.

At least one-third of the known biominerals are produced by the procaryotes but the biochemical possibilities of the bacteria are far broader than the geochemical diversity of recent natural environments. Given this fact we hope to discover a greater diversity of procaryotic biominerals in the Precambrian. Recently the first steps in this direction were taken. Isotopic composition of sulphide minerals may indicate the presence of biologically induced biomineralization as far back as 2.7 billion years ago (Monster et al., 1979). Direct evidence of the presence of magnetobacteria about 2.0 billion years ago is the recently discovered biogenic magnetite crystals in Lower Proterozoic rocks (Kirschvink, 1992). The earliest products of life activity of the encrusting manganese bacteria have been discovered in deposits 1.6 billion years old (Muir, 1978). The oldest evidence of carbonate biomineralization is represented by the slightly calcified cyanobacteria in rocks 1.0 billion years old (Riding and Voronova, 1982, 1984).

The last decade has been marked by success in the separation, identification and taxonomic interpretation of biologically meaningful organic compounds (or biomarkers) from Precambrian kerogens and hydrocarbons (Hahn, 1982; Hoering, 1987; Summons and Walter, 1990; Ourisson, 1990). A general trend in the biomarker time-distribution demonstrates their limited diversity in the Early-Middle Proterozoic and increasing diversity towards the end of the Precambrian. This approach makes it possible to construct simple «molecular phylogenetic trees» and to identify the appearance of the major known groups of the organisms in the fossil record. For example, pentacyclic triterpane hydrocarbons represent the molecular remnants of the eubacteria, some sterols represent eucaryotes, and some acyclic isoprenoids are indicative of the archebacteria (the kingdom which did not leave any morphological traces in the fossil record). There have also been discovered some unusual kinds of biomarkers, indicative of the groups of microorganims of a hight taxonomic rank which existed in the Proterozoic and became extinct later (Summons and Walter, 1990).

The study of the oldest biomarkers from the well preserved Proterozoic sediments may indicate that microbial communities of the Middle and Late Proterozoic included not only cyanobacteria and phototrophic eucaryots but, possibly, heterotrophic protozoans. There were organisms resembling recent dinoflagellates among the Late Proterozoic plankton.

The increasing abundance and diversity of megascopic fossils observed through the Proterozoic fossil record seems to reflect the rise of multicellularity, which could appear repeatedly and independently in all kingdoms of the organic world. In some groups multicellularity might be genetically preserved due to the selective advantage of large body size and individual biomass or because cell specialisation.

The oldest megascopic carbonaceous fossils, which are approximately 2.0 billion years old, may still represent the flattened remains of microbial colonies or bacterial mat fragments. Some appearance of cellular structure is extremely rarely observed. Morphologically more complex carbonaceous fossils with some possible anatomical details appear in the rocks of about 1.4 billion years old but they are becoming more complex and diverse after 0.8-0.9 billion years ago. Most of these fossils are interpreted as eucaryotic algae though some of them are considered as probable colonial procaryotes, fungi or even metazoans (Hofmann, 1992).

Of critical importance may be the recent discovery of a megascopic, spirally coiled cylindrical alga, *Grypania*, in rocks 2.1 billion years old (Han, 1991; Han and Runnegar, 1992). The fossil is interpreted as the oldest eucaryotic photosynthetic autotrophic organism.

Undoubtedly metazoan body fossils and trace fossils (or bioturbations) first appear in Vendian rocks about 620 million years old which is extremely late compared to the age of life on Earth. Most of the metazoas appeared abruptly after the great Varangerian Glaciation and spread rapidly all over the globe during the vast post-glacial transgression of the seas over the continents.

Astounishing peculiarities of the oldest known animals are: a) their large body size (up to 1 meter and more so they look gigantic compared with the small shelly fossils of the early Lower Cambrian); b) generally an absence of a mineral skeleton in the majority of animals; c) high diversity of life forms; d) high differentiation at the level of a high taxonomic rank, i.e. remarkable diversity of the body plans including some unusual ones unknown or normally rare in later metazoans; e) low diversity at the species level (monotypic genera dominating); f) domination of Radialia or Diploblastica, i.e. the animals of the coelenterate grade of organisation in the fossil assemblages; g) widespread metamerism (true segmentation) and pseudosegmentation among the forms which may be interpreted as Bilateria or Triploblastica (Fedonkin, 1987).

Interpretation of the Vendian metazoan body fossils known as the Ediacara fauna (Glaessner, 1984) has met numerous methodological difficulties for number of reasons, e.g. unusual taphonomic circumstances, poor fossil record of the Phanerozoic soft-bodied invertebrates (few forms to compare), predominance of forms with «strange» body plans (problematics or forms of uncertain systematic position), and an absence of data on the Pre-Vendian metazoans. Comparison of Ediarca fauna with recent soft-bodied invertebrates is not very easy because of the great evolutionary distance that separates them. All these aspects put the Precambrian metazoans in a position of an apparent (but illusory) phylogenetic isolation. Examples of the evolutionary ties between the Vendian and Cambrian faunas are in fact more numerous than one could suppose some years ago (Conway Morris, 1993; Fedonkin, 1994a).

Although the first specimens of the Precambrian metazoans were collected in Namibia in 1908-1914 (Gurich, 1929) it took decades to prove the Precambrian age of the fauna (Sprigg, 1947, 1949; Glaessner and Daily, 1959; Glaessner and Wade, 1966). Since the time of Darwin, naturalists were puzzled by the apparent absence of metazoan remains in the Precambrian fossil record. Darwin himself considered an absence of data on the ancestors of the Cambrian fauna as a strong and disturbing argument against his theory of the gradualistic origin of species. Attempts to explain the apparent absence of the metazoan fossil record below the Cambrian strata did not seem convincing to Darwin himself (see chapter X of the «Origin»).

This situation provided psychological preparation for the (chronologically) first approach that was developed for the interpretation of Precambrian metazoans. The fossils were considered the remains of invertebrates belonging to the same high rank *taxa* as known Phanerozoic animals (including recent ones). Other psychological aspects of this approach are based on the opinion, whish dominated for a long time among paleontologists, that the high rank system of the invertebrates seems to be the same from Cambrian to recent time. The extremely poor fossil record of soft-bodied animals in the Phanerozoic made the paleontologists look through the diversity of the recent metazoans for comparison with the Precambrian ones. Such a comparison had to be done, but along with paying attention to the prevailing body plans and the peculiarities of morphology in norm, one must pay no less attention to the small relict groups, to unusual morphological phenomena, and even to the teratology of the invertebrates to find the whole range of morphological possibilities. The norm demonstrates a more narrow spectrum of characters but affects our work as systematists rather strongly.

According to the first approach the Precambrian fauna should be placed into the following taxa: Phylum Coelenterata (classes Hydrozoa, Anthozoa, Scyphozoa, Conulata, medusae of uncertain systematic position and problematic Petalonamae), Phylum Annelida (class Polychaeta), Phylum Arthropoda (superclass Trilobitomorpha or Chelicerata), Phylum Pogonophora, Phylum Echiurida, as well as some forms of uncertain systematic position even at the level of the phylum (Glaessner, 1984).

The chronologically second approach has pointed out the dissimilarity of the Vendian invertebrates to their recent conterparts (Fedonkin, 1983). For practically all species of Ediacara fauna one can point out characters that are in disagreement with the groups of recent invertebrates with which they have been compared. Comparative body plan analysis of the Vendian body fossils, with special attention to their symmetry as the result of the basic growth pattern, to the preservation, and to the mode of life has led to a different view of the system and the early evolution of metazoans in the Precambrian (Fedonkin, 1985, 1987, 1992, 1994a). In particular, three new classes of the coelenterates were established (Cyclozoa, Inordozoa and Trilobozoa), a new Phylum Proarticulata (with the classes Dipleurozoa and Vendiamorpha), and new arthropod class Paratrilobita (Fedonkin, 1985, 1990).

The third approach underlines an unusual taphonomy and architecture of the Vendian body fossils considering most of them as representatives of the non-metazoan Kingdom Vendobionta (Seilacher, 1989). Sandy exoskeletons of an extinct group of botom-dwelling sea anemones (Psammocorallia) and the trace fossils represents «true» metazoans (Seilacher, 1990). Critical analysis of the concept of Vendobionta has been published elsewhere (Gehling, 1991, Fedonkin, 1992, 1994a, Conway Morris, 1993).

Though the system of the Vendian body fossils is under an intensive discussion the key arguments in favor of their metazoan nature are being received from taphonomic and paleoecological study, and from the comparative promorphological (Bauplan) analysis of these fossils and their later counterparts.

What are the major revelations of life in the light of the Precambrian fossil record?

1. The Phanerozoic fossil record embraces less than 15 per cent of life history. The ages of Earth and life are comparable. This fact returns our attention to the old idea of panspermia and to the statement by V.V. Vernadski that «life is geologically eternal».

Taking into account the preservational aspect of the Precambrian fossil record (the older the deposits the less paleobiological information is preserved) and the ecosystem principle of the life maintaining (from the very early moment the life should exist as an ecosystem uniting the organisms with the different trophic and biogeochemical functions) we should talk about the appearance rather than the origin of life on Earth. One cannot rule out the possibility that the question on the origin of life might be posed incorrectly. The paleontology of the Precambrian revives this problem though its resolution may be beyond the scope of paleontology.

2. During the major portion of life history the procaryotic ecosystems have dominated absolutely in the most of the habitats. However, neither morphologically nor ecologically have the procaryotes changed much during 3.8 billion years since they first appeared in the fossil record. This may be particularly true for the cyanobacteria which have a preservational potential that is higher than that of other procaryotes because of their larger cell size and their ecological peculiarities.

3. The history of the biosphere can be subdivided into two parts. The earlier and longer period of time was marked by the dominance of conservative bacte-

rial ecosystems and by gradual and steady changes in the abiotic parameters of the environment. The environmental change was essentially produced by the biota. The later and shorter aeon is characterised by the rapidly evolving eucaryotic organisms and by the relatively stable abiotic parameters of the environment controlled by the biota.

4. A two-stage structure of the global biota consisting of a conservative and stable procaryotic «foundation» and an extremely changeable eucaryotic «building» or «epistructure», was effectively formed during the Late Proterozoic. The eucaryotic trophic pyramid was built above the pre-existing network of biogeochemical interactions between the microbial communities. This additive phase in the evolution of the global ecosystem was relatively short. The substitution of the individual members in the eucaryotic trophic hierarchy became the major process in the subsequent history of the global ecosystem which retained its principal structure.

5. The world of diverse eucaryotes is in fact an epiphenomenon on the procaryotic ecosystems. Thus, evolution in a Darwinian sense as well as the phylogeneses seem to be relatively late phenomena of the life history. The phylogenetic tree as a symbol of irreversible and divergent mode of historical development reflects the late and shorter part of life history which was predated by longer periods of mosaic or network «evolution».

6. Though the phylogenetic roots of the eucaryotes go as far as 2.0 billion years ago these organisms did not play an essential role in the global ecosystem untill the Neoproterozoic. For a long period of time since the moment of their appearance the eucaryotes seemed to stay in the limits of their primary biotopes.

7. The primary biotopes for eucaryotic cells could be the microenvironments with sharp geochemical (and/or light and thermal) gradients and consequently with different procaryotic populations closely spaced. The symbiogenetic origin of the eucaryots was in fact the process of the miniaturization of the pre-existing procaryotic ecosystems dowm to the size of the cell.

8. In spite of the incredible tollerance of the procaryotes to a wide variety of the environmental factors and their ability rapidly to restore an optimal population density they were forced out as the dominants from most of their habitats by the eucaryotic organisms at the end of the Proterozoic. Eucaryotes have opposed their ability to evolve at the species and ecosystem levels, their stupefyng diversity, more active metabolism and larger individual biomass. But what is more important is that the eucaryots have created longer trophic chains. More complex ecosystems turned out to be more economical energetically.

9. The relative simplicity of trophic systems, and the determinate and conservative character of the biogeochemical and reproductive reactions of the procaryotes to the abiotic factors of the environment make it methodologically easier to decode the biogenic signals from the Precambrian fossil record of the procaryots than from the Phanerozoic one. Being masked by the eucaryotic epistructure the Phanerozoic world of the procaryotes remains obscure. Classical Phanerozoic paleontology is traditionally oriented to the eucaryotes mainly because of their high preservational potential, great diversity and evolutionary change (i.g. the factors important for biostratigraphic purposes). However, one should take into account that the rise of the eucaryotes was the cause of the destruction and deformation of the procaryotic fossil record.

10. An actualistic approach to the interpretation of the Precambrian procaryotic communities and their habitats leads to the non-actualistic model of the global environment.

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Charles Darwin, Fritz Müller, Anton Dohrn, and the origin of evolutionary physiological anatomy

Abstract — Darwin brought a truly historical perspective into evolutionary biology that differed fundamentally from formalistic and orthogeneticist notions of change. His approach to historical reconstruction was strongly influenced by his geological research. Scenarios in his monograph on barnacles illustrate his physiological approach, with functional continuity playing a major role. His ideas on the relationship between ontogeny and phylogeny were later taken up and applied to other crustaceans by Fritz Müller before Haeckel developed the same theme. Anton Dohrn, who also worked on crustaceans, owed much to Darwin for his physiological approach to phylogenetics, especially the principle of Funktionswechsel or succession of function. The tradition continued with the Russian school of evolutionary morphologists, notably Sewertzoff and Schmalhausen.

Among the many myths in the history of evolutionary biology is that nothing of great importance happened to comparative anatomy when Darwin came along. Like a lot of myths, it has a certain foundation in fact. Comparative anatomists could indeed get away with proceeding just as they always had, and some of them did. For many, the changes were superficial — perhaps little more than acknowledging that taxonomic groups have common ancestors. For some, the very denial that there was a Darwinian revolution in comparative anatomy, or even that such a revolution is possible, has been one way of opposing such changes. For others, it has been a means of stressing the very novelty of Darwinian thinking, and the conservativeness of the opposition.

Here I shall argue that something of great significance really did happen to comparative anatomy as a result of Darwin's work. Darwin recognized that it had, and he acted upon it. So too did some of his supporters, and the consequence were momentous. If their accomplishments go largely unacknowledged, it is partly because they seem all too obvious, and partly because they have been forgotten, if not outright suppressed.

The very refusal to recognize important differences between pre-Darwinian and Darwinian attitudes toward nature would seem to reflect a persistence of those very attitudes that Darwin called into question. To Darwin's predecessors, change was something to be denied, or at least minimized. If not downright illusory, it was superficial and not very important. To Darwin, on the contrary, change was not just important, it was the fundamental reality. Natural selection produced things that are novelties in a deeply metaphysical sense, one that was lacking in earlier thought.

Let me contrast the old way of thinking with the new, albeit with the proviso that I have to simplify a bit for the sake of clarity (see Ghiselin, 1980). Pre-Darwinian biologists were perfectly aware that change of a sort occurs in the ontogeny of individual organisms. The term «evolution» originally meant embryological development, and the «development hypothesis» was often used for the views of Lamarck and his followers. Efforts to deal with evolution in our modern sense were largely based upon analogies with evolution in the older, embryological sense. There were two basic ways of thinking about an ontogeny, namely preformation and epigenesis. In either case, things went from one particular condition to another particular condition — from A to B — unless, perhaps, something interfered with the normal state of affairs. Change was not «real» insofar as everything was pre-ordained. For preformationists, ontogeny was a sort of «unfolding» or a change from a condition of potentiality to one of actuality. For epigeneticsts, ontogeny was the result of the action of supposed laws of nature, and was often analogized with the growth of a crystal. Here, change would not be real, insofar as the laws of nature are eternal; a crystal of a given kind will precipitate out of solution whenever the necessary and sufficient conditions are met.

When such notions are translated into an evolutionary context, one gets somewhat different versions of what is often called «orthogenesis.» In the preformationist version, the changes that might be called «evolutionary» were attributed to the will of an omnipotent and omniscient Being, who foresaw and indeed pre-ordained everything. In the epigeneticist version, that same Being ordained the laws of nature, with much the same general effect. As one might expect, such thinking was both vague and flexible, so that one might invoke a wide range of positions with respect to what might cause the changes in question. Often unknown «laws» or mysterious «forces» or «tendencies» were invoked.

Once we realized that such notions of causality were presupposed, it is most misleading to label such pre-Darwinian figures as Buffon, Lamarck, or Owen «evolutionists» in our modern sense. It is also easy to see why Darwin, like many other scientists, considered such quasi-evolutionary notions unscientific. Miracles and occult forces were not amenable to scientific investigation. Darwin, to be sure, believed that ontogeny plays an important causal role in evolution. But like us moderns he believed that whatever it is that causes ontogeny also evolves. And like us moderns he believed that evolution is governed

by laws of nature. Much of his research was aimed at discovering such laws.

Darwin was an «evolutionary physiological anatomist» in the sense that he explained life as the consequence of the vital activities of real, concrete organisms, through time. The physiological aspect of Darwin's evolutionary biology is not always appreciated. His classic work on plant movements is highly esteemed by physiologists. However, the evolutionary aspect of this work is only apparent when one considers his little book on *The Movement and Habits of Climbing Plants* (Darwin, 1865). Here he provides scenarios for changes in both behavior and anatomy. I mention this work primarily to make the general point that Darwin was anything but a «formal morphologist» or someone who believed that studies of form should be divorced from studies of function. Indeed the term «functional morphology» is an oxymoron if the word «morphology» is used in its strict and original sense.

Darwin was also a geologist, and this further distanced him from formal, and *a fortiori* from idealistic, morphology. During his trip around the world Darwin carried out extensive geological research under the influence of Charles Lyell's *Principles of Geology*. This research was of crucial importance, for it gave Darwin a great deal of first-hand experience in the kind of historical thinking that he would later apply to biology. Although Lyell did not himself believe in evolution, the kind of thinking that he advocated only had to be carried a little further to transform biology into the sort of historical science that geology had already become. Lyell had a «steady state» view that limited the amount of change, and Darwin had to reject that. But the notion that change is gradual could easily be accommodated in a biological context. More fundamental was the point that the laws of nature, which do not change, can be used to reconstruct past events. If one knows a law of nature, then one knows what can and cannot happen at any time whatsoever. Consequently a geologist can ask what possible events might explain the present configuration of the earth, and rule out some of the possibilities on the grounds that laws of nature rule them out. Or to put it more loosely, the narrative theories gained plausibility when they were shown to exemplify broad generalizations. Darwin's coral reef theory is clearly based upon «global» considerations, much as is modern plate tectonics. How much these more basic generalizations are laws and how much they are particulars is a question that deserves further consideration.

Another important benefit that Darwin gained from studying geology was the habit of conceptualizing problems in terms of concrete objects and real events. Even though geologists' diagrams can be schematic, there is rarely any doubt that they are diagrams of real rocks and strata, not diagrams of «rock» in the abstract. Systematists were much more apt to treat groups of objects as abstractions, and both their language and their diagrams had a strongly metaphorical character. So although some of Darwin's predecessors drew «tree-like» diagrams, these rarely if ever had the connotations of a nexus of real parents and offspring. They were merely a way of expressing the notion of similarity and difference. Likewise there was a profound difference between the «archetypes» of idealistic morphologists like Oven, which were abstract schemes, and the so-called «archetypes» of Darwin, which were real organisms that must have metabolized and done all those other things that organisms do.

Darwin's work on Crustacea provides excellent materials for studying his phylogenetic methodology. Although it was published before Darwin publicly announced his evolutionary point of view, there is no question that his *Monograph on the Sub-Class Cirripedia* (Darwin, 1851, 1854) was a work on evolutionary systematics. We know this from his correspondence, as well as from his commentary in *The Origin of Species* and elsewhere. Furthermore, and this is very important, his contemporaries, including Crustacean systematists who were among his most enthusiastic supporters, read the monograph as straight-forward phylogenetics. They applied his methods to similar material. Because the monograph has been foundational for all subsequent work on the group, students of barnacles have provided some excellent commentary. The latest analysis by Newman (1993) is an outstanding example, and one to which the present discussion owes a great deal. (See also Ghiselin, 1969; Burkhardt and Smith, 1988).

Darwin of course was fully aware of the fact that his predecessors had been able to create «natural systems» of classification with hierarchies of groups within groups that shared diagnostic characters. The classification in his barnacle monograph bears out the position he took in the *Origin* that classification should be strictly genealogical, though he allowed for «paraphyletic groups» (ones that do not include all of the descendants of the common ancestor) to express the «amount of difference» (Ghiselin and Jaffe, 1973). In later publications he took a stronger position in favor of strict monophyly (Ghiselin, 1985). When one thinks in terms of taxonomic groups, strict monophyly allows one to avoid mistaking a group that has undergone much divergence for one that branched off early. This same mistake, however, can be avoided by using «tree thinking» rather than «group thinking» (O'Hara, 1988). If one thinks in terms of trees, one also thinks more clearly about what characters are really important, including the ones that are «derived» or as cladists say «apomorphic». Darwin did not discuss such matters explicitly, and he seems to have taken a rather «common-sensical» approach, much as he did in geology. His basic classification has not been much revised as more has become known about the group and as genealogical classification has become increasingly popular within systematics in general.

It is of considerable interest that for Darwin the diagnostic feature of the Cirripedia was attachment of the cyprid larva by a particular kind of highly-modified «antenna», definitely a derived condition. He justified this character on the basis of its «high physiological importance» and there being no strict precedent for it in other groups. It would seem that for cirripedes «high physiological importance» means a kind of technological breakthrough that allows the further evolution of the group (a key innovation), and for something that lives as they do, such an adaptation is not likely to be secondarily lost. Whether the complexity of this attachment organs was seen as a criterion for considering it most unlikely to have evolved more than once is something I cannot answer at the present time. However this ex-

ample suffices to refute the notion that Darwin believed that classification should be based only upon characters of trifling physiological significance. He did think that his theory could explain why some characters with no obvious utility were often of high diagnostic value, but that is a very different issue.

Darwin's scenario for the origin of cirripides invoked as a common ancestor a rather advanced crustacean that fed with its feet then became attached by its antennae and subsequently underwent much modification. Given that the animals were very different from other crustaceans, one might take this to mean that they were an early branch of the Crustacea. But Darwin made no such mistake, and this negative evidence is significant. For him the question of relationship was not a matter of similarity, but of whether there might have been intermediate forms. Such intermediates also had to be physiologically viable organisms, not just morphological intermediates. In his debate whith Étienne Geoffroy Saint-Hilaire, Cuvier invoked the implausibility of functionally viable intermediates as a means of ruling out the derivation of one kind of organism from another, and his arguments were perfectly legitimate in that context. However, Darwin and his followers turned the argument on its head, and used the argument from physiological continuity as a means of phylogenetic inference. One goes back to the most recent plausible common ancestor that would not be excluded by such considerations. He believed that he had found what we would call the «sister group» of cirripides well within the Crustacean phylogenetic tree. Thus he seems to have reasoned by putting things together on the basis of shared characters, rather than by separating them on the basis of differences.

In considering Darwin's «model» for the origin of the Cirripedia, one might wonder to what extent the scenarios are merely an afterthought to tree-like diagrams established upon some other basis. Or are they are something constitutive, in the sense of providing support for the trees themselves? I believe that Darwin would have answered that they are indeed constitutive. The ancestral cirripede itself may not be a good example of this. However, the use of functional criteria for establishing homologies which are in turn evidence for relationships, is commonplace in Darwin's work. So far as he could, he tried to derive new structures from pre-existing ones, perhaps with a change in function. We face a problem here. Darwin gives two examples of the origin of such features in cirripedes, and they both turn out to be mistaken: the cement glands and probably the ovigerous frena (Walker, 1983). There are plenty of good examples, however, and such «plausibility arguments» are by no means uncommon in phylogenetic reasoning. I will come back to them later when I discuss the contribution of Dohrn.

The principle of functional continuity can be derived from the theory of natural selection, but it is also consistent with any theory that entails the viability of hypothesized organisms in a sequence of real ancestors and descendants. Natural selection, however, specifies conditions under which certain kinds of changes do and do not occour, and therefore can be invoked to rule out certain kinds of changes that otherwise might seem possible. Natural selection cannot adapt a population to selection pressures that it has not yet encountered, or, to put it in more literary language, it has no foresight. The most clear-cut example is vestigial organs, which have to be interpreted as parts that are in the process of being lost, rather than gained. Advocates of orthogenesis, especially preformationist versions, have not been thus constrained.

Darwin discussed the importance of vestigial structures for phylogenetic research in the *Origin of Species*. He had extensive experience with them in his work on barnacles. Such structures were particularly evident in the dwarf males that he found associated with hermaphrodites and fermales in certain lepadomorph barnacles. What use he made of vestigial parts in reconstructing the evolutionary history of the group is not always clear from the text, and some of the examples may seem a bit obscure. He thought he saw vestiges of missing segments in the cypris larva. In *Chelonibia*, a pair of vestigial sutures convinced him that the «rostrum» of higher balanines had been formed by the fusion of the true rostrum with the adjacent plates.

A more straight-forward example of functional reasoning is seen in his decision that the males in cirripedes are hermaphrodites in which the female parts have been lost, and which have subsequently been reduced. It makes a lot more sense for a tiny, and often gutless animal with appendages that are reduced or missing, single gonads and no intromittent organ to be the endpoint of regressive evolution, rather than the beginnings of a more complicated creature. Furthermore, Darwin believed, as we do, that the males in barnacles had been produced by a mechanism called «progenesis» involving loss of later developmental stages and early sexual maturation.

This brings us to a consideration of Darwin's views on the relationship between embryology and evolution. In addressing this topic it should be stated at the outset that there are serious problems with the literature on the relationship between ontogeny and phylogeny. Much of it has been written by persons who have little if any sympaty with phylogenetics as a topic for scientific research. This is particularly the case with advocates of «experimental» approaches. The problem is exacerbated by factional disputes among systematists. A great deal of mythology has been built up, and therefore it is essential that one go back and consult the original documents, especially those that are neglected in the secondary literature.

In his *Autobiography* (Barlow, 1959:125) Darwin expresses dismay at how little attention was given to what he said about the relationship between ontogeny and phylogeny in the *Origin of Species*, where, he believed (and I think rightly), he had provided the basic solution to such problems. He goes on to say that «Within late years several reviewers have given the whole credit of the idea to Fritz Müller and Häckel, who undoubtedly have worked it out much more fully, and in some respects more correctly than I did.» Subsequently Müller has been largely forgotten. But Müller gave Darwin full credit, and the importance of Müller's contribution was widely recognized by his contemporaries.

During the 1830s and 1840s Darwin familiarized himself with the views of his predecessors as he developed his own. He was well aware of what those views were, although he often relied upon secondary sources. He could not accept their explanations for

the relationships between embryology and classification, which contradicted not only his own theory, but his very idea of what constitutes a legitimate scientific theory in general. Both the preformationist and the epigeneticist versions of «recapitulation» had to be ruled out. However, given that developmental processes evolve as a consequence of selection, he could explain the observed phenomena and therefore use them as evidence in favor of his theory. In the context of phylogenetics this meant that the development of an organism might contain valuable clues as to its ancestry.

According to Darwin's theory, variations arise fortuitously (not at random in the sense that one variation is as probable as another) at any stage in development. If passed on to the next generation, they tend to appear at the same stage as they did in the parent. Variations accumulate as a consequence of selection, the nature of which is contingent upon the conditions of existence. So both 1) the time in ontogeny at which a variant appears and 2) the time in ontogeny at which its presence affects fitness are capable of affecting how the entire life cycle will evolve. Early variants or early selection could produce early divergence, perhaps conpled with late divergence as well. But if selection in different lineages was on late variants or late in the life cycle, or both, the young stages would remain unaltered. Which of these happened in any particular case would be a matter of (contingent) historical fact, and would have to be worked out by historical biologists. If laws were to be used in such reconstruction, they had to be the laws that govern variation, selection, and other processes. Darwin believed that an understanding of developmental mechanisms would help. But there was no way in which he could simply conjoin a description of an organism's ontogeny with a statement of relevant laws and infer its history.

One might question whether the above reconstruction of Darwin's views is correct. It is justified by the general pattern of his procedures as well as by his explicit statements. In the *Origin of Species* Darwin gives a succinct account of his views, one that was perhaps too brief for many readers to have understood it (Darwin, 1859:439-450). His detailed exposition of his views on the relationship between embryology and evolution is explained in *The Variation of Animals and Plants under Domestication* (Darwin, 1868), a work that is rarely even mentioned in this context. Indeed, because it is wrongly considered a book on heredity, and one that contains a theory that is no longer credible, it is virtually never read by anybody (see Ghiselin, 1975). Darwin derived his views on developmental physiology from his readings of works on plant and animal breeding, teratology and related subjects, through conversation and correspondence with many informants, and from his own empirical research. In the book on *Variation* he gives examples of changes occuring at various stages in the life cycle. It is important to stress that they are not limited to the end of ontogeny, as strict recapitulationism would have it.

In the *Monograph on the Sub-Class Cirripedia*, we find clear applications of Darwin's embryological principles to phylogenetic analysis. Of course he used these principles together with all the other evidence that was available to him. Dana and Milne Edwards had divided most of the Crustacea into three groups which Darwin evaluated as the possible closest relatives of the Cirripedia: Entomostraca, Edriopthalmia, and Podopthalmia. He opted (1854:13) for the last of these, the «stalk-eyed» crustaceans, on the basis of various characters, including details of the structure of the carapace and its derivates. Within the Podopthalmia he noted that there was an «aberrant group of low organisation» (1854:18) which combined a mixture of entomostracan and podopthalmian traits and had more in common with the Cirripedia than any other group. The group included *Phyllosoma*, which turned out to be larvae of palinurids (spiny lobsters) and *Amphion*. This group he said (1854:19) «leads into the Stomopoda», which included *Lucifer*, Darwin's model for a cirripede ancestor. *Lucifer* is a pelagic animal, now placed in the order Decapoda and suborder Dendrobranchiata (=Penaeidoidea), and includes *Amphion*. How close a relationship he invoked is not clear from Darwin's text. However, his views on the homologies of limbs provide a good reason for relating the Cirripedia to an early offshoot of the malacostran lineage. Namely, he thought that the last cephalic and first thoracic segments in cirripedes had been reduced (1854:111), rather than the last two thoracic segments as was the opinion of Dana (Darwin, 1854:22) and later authors. He thought he had some evidence for this in the reduced condition of these limbs in *Phyllosoma* and allied forms (1854:18); and this view seems to have been justified by reference to the work of Henri Milne Edwards (1834-40) whose «Stomapoda» included what are now called «Stomatopoda» (Hoplocarida», and mysids, as well as *Lucifer* and some larval forms.

The figure of *Lucifer* that appears in Darwin's monograph (1851:28) was copied from Milne Edwards (Pl. 28). Below it Darwin presents a drawing of «a mature Lepas, with the antennae and eyes, which are actually present in the larva, retained and supposed to have gone on growing». The claim of Richards (1992) that this is a larval crustacean is an egregious blunder, and the work is seriously flawed in other respects as well (Ghiselin, 1992). For Darwin, the cirripedes were a group of early malacostracans that became sessile filter-feeders and then underwent considerable reorganization and subsequent adaptive radiation. Both progressive and regressive changes were involved, and the scenario presented was anything but orthogenetic.

Among the «regressive» changes that Darwin invoked were the regression of parts among parasitic forms. When Darwin invoked the «arrest» of development in simple animals he really meant that something previously present had ceased to develop; this is fundamentally different than the claims by some of his predecessors that simple animals have not undergone the sort of ontogeny that the more complex ones might. So when he refers to the «Apoda» as «larval» he is talking about progenetic animals. In his scenario for the evolution of dwarf males from hermaphrodites, he treats the reduction of the males as a case of progenesis, which is a modification of the developmental mechanism. He justifies the invocation of progenesis by reference to the histological appearance of the tissues of the males: they look like those of larvae, not adults. So although the reduction of the males was supported by conventional synapomorphies, strictly physiological criteria

were also invoked. Further processual evidence for the reduction of the males was provided by vestigiality of parts, and by the general plausibility of adaptive change in the mode of reproduction.

If we want to find evidence that Darwin produced some kind of change in the lives of comparative anatomists, we ought to examine the work of those who were most likely to understand his views, those who not only accepted his theory, but embraced it with unqualified enthusiasm. A particularly good example is Fritz Müller (1822-1897). His discovery of Müllerian mimicry is good evidence that, unlike most nineteenth century «evolutionists», he understood natural selection very well. If anything, his politics and his religion disposed him to favor natural selection and its implications, for left Germany upon religious grounds in 1852, and spent his remaining years in Brazil. He did a great deal of research on the anatomy, embryology, and phylogenetics of various marine organisms, especially crustaceans. He presented his work on crustaceans as a kind of test of Darwin's theory in his book *Für Darwin* (Müller, 1864), which pleased Darwin so much that he had it translated into English as *Facts and Arguments for Darwin* (Müller, 1869).

Müller provides various arguments for Darwin, including evidence for sexual selection in the form of «high-low» dimorphism among Tanaidacea (Malacostraca: Peracarida). He shows clear evidence of having given a great deal of thought to what now is called «character analysis» in a cladistic context. He shows by (p. 7) a pair of what can only be called «cladograms» two lines of evidence, on the one hand a large, asymmetrical chela that might be a good synapomorphy for several species, and, on the other hand, the absence of a second branch to the first antennae that might be a convergent loss. But this discussion is rather fragmentary and does not explicity address such issue as plesiomorphy and the use of outgroups.

Müller presents a most impressive effort to apply Darwin's ideas about the relationship between ontogeny and phylogeny to the Crustacea. He recognized two basic kinds of larvae, the nauplius and the zoea, which may exist in the same life cycle. In the most primitive crustaceans then known, the Phyllopoda (as then understood, roughly equivalent to our Branchiopoda), a nauplius stage is followed by an adult stage which is essentially equivalent to a zoea, but lacks the modifications that occur in both the zoea and the adult of higher crustaceans (so that there are a long series of relatively undifferentiated appendages). In higher crustaceans the zoea has its characteristic features and the adult is more modified in structure. Müller (1869) had established that a group of highly degenerate internal parasites of crustaceans, the Rhizocephala, are closely related to the Cirripedia, and had done so mainly on the basis of their characteristic larvae, the oldest of which have some features suggestive of a zoea. He proposed that the Rhizocephala are what we now would call the sister group of the true barnacles (Thoracica), as is generally maintained today. Barnacles have nauplii and a «cypris» or cyprid larva, so-called because it resembles an adult ostracod. Darwin called the cypris a «locomotive pupa» and the term expresses its function as a specialized, non-feeeding stage that settles and undergoes metamorphosis into the juvenile. Müller (1864) dismissed the resemblance to ostracods as convergent. According to Newman (1983) the traces of a zoea in the Maxillopoda (Copepoda, Cirripedia, Ascothoracica, Branchiura, Mystacocarida, and Ostracoda) are real, and the Maxillopoda are a clade related to the «urmalacostracans» that have undergone a loss of segments due to progenesis.

Fritz Müller clearly and emphatically rejected the efforts of Johannes Müller, Louis Agassiz, and, without naming him, Karl Ernst von Baer, to explain the parallels between the taxonomic hierarchy and the sequence of development in crustaceans in terms of what he dismissed, explicity, as scholastic philosophy. Rather, he adopted and developed the interpretation that Darwin had presented in the *Origin of Species*. Observing that variations might occur early or late in ontogeny, he explained that there might be very different results. An animal might deviate early in ontogeny; in that case it would retain the original condition only for a short period. Or it might add new stages at the end of ontogeny; if so ontogeny would pass through the series that mirror the history of the species. The important point here is that «terminal addition» is the one condition under which recapitulation applies in a straight-forward manner. He also concluded that the phylogenetic evidence may get obliterated when development becomes direct, or it may get falsified as a result of natural selection undergone by free-living larvae. In order to infer what the actual history had been, one had to apply some principles and rules. Arthropods with more pronounced metamorphosis had probably deviated more than others from the ancestral condition, as had those with greater difference in way of life – the two, of course being strongly correlated.

Müller goes on to interpret the development of the Malacostraca in the light of this theory. He proposed that the zoea larva gives the best picture of the ancestry of the group. He thought that the nauplius larva had been obliterated in these higher Crustacea, although he found traces of it in the relatively primitive *Mysis*. Spines on the zoea he interpreted as defensive adaptations that had arisen in the larva. Gradual differentiation of segments toward the posterior was treated as the ancestral condition, whereas simultaneous differentiation of these was the result of a condensation and simplification of development. Müller does not provide anything like an «algorithm» for dealing with such problems. A great deal of ingenuity would seem to be involved. However it is clear that he recognized from the outset that the history of the lineage cannot be read off in a straightforward manner from ontogenetic data.

It is easy to see, however, that people might read the works of Darwin and Müller and ignore or forget the difficulties. Or they might get their information from other sources such as Ernst Haeckel (1834-1919). Even if people read such technical works as the *Generelle Morphologie* (Haeckel 1866) his popular writings obviously oversimplified matters. Haeckel was also a very effective teacher, and his students naturally learned Haeckel's version of what was called Darwinism. It emphasized morphology and recapitulation rather than the kind of functional thinking that was so characteristic of the work of Darwin himself.

One such student of Haeckel was Anton Dohrn (1840-1909). He began his career as an entomologist, then, as a result of reading the work Fritz Müller,

switched to Crustacea, a move that put him in a good position to understand Darwin's approach. Initially Dohrn was very enthusiastic about ontogeny as evidence for phylogeny, but his own research as well as that of other workers ultimately proved disappointing. Müller had suggested that the zoea might have given rise to the insects, and Haeckel endorsed this view. Dohrn thought he had found vestiges of the zoea's defensive spine in insect embryos, but ultimately had to give that up.

In 1870 Dohrn published an anthology of papers that he had recently published on arthropod phylogenetics. The introduction to the second half speculated, noncomittally, that the Arthropoda might be polyphyletic. In 1871 he published the first part of a paper, one that was never completed, that represents at once the end of his earlier, ontogenetic, approach and the beginning of his new, physiological one. On the one hand it treats the phylogeny of the Crustacea from a strongly recapitulationist point of view. The nauplius is compared to larval annelid and treated as the ancestral form. The zoea is an modified nauplius, which had added segments at the posterior and of the body. If the recapitulationist account were true, this made sense from a physiological point of view — as an adaptation to increasing body size.

Invoking such functional explanations, Dohrn developed an adaptive, physiological scenario for the phylogeny of the Crustacea. He attributed a great deal to the division of labor among appendages, and to the various appendages changing their functions. His scenario also includes the complete loss of certain features, such as the nauplius and the zoea in ontogeny and the carapace and the eye stalks in the adult. When he did so he related such changes in environmental circumstances, such as moving into fresh water or to a benthic habitat. The ostracodes had undergone a secondary reduction in size, and were therefore secondarily simplified in some respects. A second fragment of this work appeared as an appendix to his book on the origin of vertebrates (see below). He tried to account for the origin of the Rhizocephala using *Anelasma*, a parasite of sharks as a model. The scenario was indeed plausible, but there were two problems. First, he put the solution to the problem in the hands of Robby Kossmann, who did the empirical work and got the credit (Kossmann, 1873). Second it makes sense as a sort of model, but the rhizocephalans evidently branched off much too early to be directly derived from whithin this particular group.

Dohrn's functional explanations for the evolution of crustaceans were by no means unreasonable, and ones like them have continued to play an important role in crustacean phylogenetics. The main problem with his phylogenetics was not the functional aspect, but rather that the strict application of the recapitulationist view became a kind of procrustean bed, and the notion that the nauplius and the zoea represent adult ancestors became increasingly untenable as data on crustacean larvae accumulated. His critics pointed out, and Dohrn admitted, that it would be easier to start with an annelid having many segments as the ancestral precursor of the arthropods, and have something like that evolve an exoskeleton. Then it became a fairly straightforward matter to develop a scenario in which the adult crustaceans had undergone the sort of division of labor and functional reorganization that Dohrn had envisioned. And there would still be a place for evolving larvae and changes in size in response to changing conditions of existence.

Once we see that the embryological program was breaking down, it makes a great deal of sense that Dohrn would emphasize the physiological approach even more strongly. The connection between his work and that of Darwin is easily established. They began to correspond about crustacean phylogenetics in 1867 and met at Darwin's home on September 26, 1870. Much of the extant correspondence (Groeben, 1982) relates to the founding of the Zoological Station at Naples, which was a work of administrative and organizational genius, but one that diverted Dohrn's attention from the sort of phylogenetic work that was the *raison d'être* for the laboratory itself.

Darwin, who was an enthusiastic supporter of the laboratory, sent Dohrn a copy of *The Expression of the Emotions in Man and Animals* (Darwin, 1872). It arrived on November 13, 1972. Dohrn read it immediately. His review of this book, in English, appeared the following summer (Dohrn, 1873). *The Expression of the Emotions* is a very good specimen of Darwinian evolutionary psychology and evolutionary physiological anatomy, and Dohrn rightly interpreted it as an example of how that kind of science might be done. For example, the bearing of teeth, originally preparatory to combat, persists as an emotional expression or signal. Dohrn suggests that the «book derives its chief interest from being a successful attempt to trace the origin of special functions, to introduce the theory of Evolution into the domain of physiology». He proposes that the practice of separating morphology from physiology is no longer possible, and «that the new task of physiology will be to investigate the origin of functions.»

Darwin's theory had come under attack by one of his most skillful critics, Saint George Mivart (1871), among other things on the grounds that Darwin had no explanation for the origin of new structures. Actually Darwin had anticipated this criticism, and responded more fully in later editions of the *Origin of Species*. Henri Milne Edwards (1851a) had maintained that organs could be «borrowed» from unrelated groups, but Darwin of course realized that he had to rule out such notions if his theory was true. New organs had to evolve from pre-existing ones, and as suggested above, he used this assumption as a guide to phylogeny. Be this as it may, Dohrn was provoked by Mivart's criticisms, and wrote an essay entitled *Die Ursprung der Wirbelthiere und das Princip des Functionswechsels* (Dohrn, 1875), which Dohrn translated, in a letter to Darwin dated February 7, 1875 as *The Origin of Vertebrates and the Principle of Succession of Functions*. His use of the word «succession» instead of «change» for the German *Wechsel* is significant, for it suggests that the process is a very orderly one. And indeed this is clear from the text. An organ or other part starts out having a main function and a subsidiary function. In response to selection, the subsidiary function becomes increasingly important relative to the main function, and finally becomes the main function, and, as a result, the entire organ is transformed. We now have plenty of examples of this sort of transformation, and it is a common part of our scenarios for the evolution of things like mammalian inner ear bones. Having a scenario

in which the intermediates change through a series of functionally plausible intermediates with an orderly replacement of functions is one canon of evidence that at least some phylogeneticists endorse. And the principle is generally accepted as a major contribution to the study of evolutionary mechanisms, although often ignored by phylogeneticists (Mayr, 1960).

Dohrn illustrated his principle by means of concrete examples that have largely been refuted and many of which were excessively speculative even at the time. He tried to derive the vertebrates directly from annelids, and to make the tunicates degenerate vertebrates. The annelid theory in one form or another remained viable for quite some time, and in that sense was by no means a failure. Indeed, new molecular data have made some sort of annelid theory a very good possibility. Segmentation in both protostomatous and deuterostomatous eucoelomates is controlled in ontogeny by very similar mechanisms, and sequence data on ribosomal RNA indicate that segmentation was more widespread than has been thought (Ghiselin, 1988).

Dohrn also got considerable credit for the notion that a great deal of regression takes place. But although Dohrn's scenarios for vertebrate evolution were suitable from the point of view of explaining his physiological principles, they were highly speculative and not the sort of thing that would be accepted without much further evidence. This left him open to attacks by hostile critics, including Haeckel and Gegenbaur.

As the director of the most important zoological laboratory in the world, Dohrn was in an excellent position to push on with empirical research and to get his views known through personal contacts and publication. Visiting investigators naturally took an interest in Dohrn's work and helped to publicize it. Furthermore he had a scientific staff that helped to run the Station and also did research. This included work on taxonomic monographs that appeared as the *Fauna und Flora des Golfes von Neapel und angrenzenden Meeres-Abschnitte.* The third of these monographs was by Dohrn (1881) and dealt with the Pantopoda. Dohrn was by no means through with the arthropods.

The Pantopoda, or Pycnogonida, are commonly called sea spiders, although their relationships to true spiders and other aracnids are highly problematic even today — and largely for the same reasons that they were both a challenge and an opportunity to Dohrn. Highly modified arthropods, with small bodies and long legs, they do have sort of a spider-like appearance. To explore this possibility, one might try to see if they had the same general arrangement of limbs and segments as a spider or other arachnid. Proceeding as comparative anatomists usually do when dealing with such problems, one might look at the front end of the body and find a pair of claw-bearing appendages that look like chelicerae, followed by a pair of what look like pedipalps, of a spider or other arachnid. Then one might observe that at the rear there are four pairs of walking legs, again, like a spider or other arachnid. The trouble is that there is one additional pair of appendages between the first two and the last four. Much of the history of pycnogonid comparative anatomy has been an effort to account for that extra pair of limbs, and just about everything one might think of has been suggested: loss of a segment in arachnids, duplication or subdivision of a segment in pycnogonids, non-homology of the posterior four pairs of limbs. The comparative anatomist's problem is rendered all the more frustrating because the posterior end of the body has been reduced, and because there may be several genital openings rather than a single pair located in a place that is diagnostic of some other group of arthropods. In the middle of the nineteenth century that generally meant the crustaceans, though we should point out that at that time Crustacea was often used in a broad sense that included such things as trilobites and *Limulus.*

Dohrn (1869) had studied the embryology of pycnogonids in some detail during a visit to Scotland in 1868. He found that the young stage has three anterior appendages, and, in conformity with his basic approach at the time, concluded that this larva was a nauplius. However, although later development seemed like that of crustaceans, he found no sign of a zoea, which would be diagnostic of the Crustacea. Therefore he concluded that although the pycnogonids are related to the Crustacea, they branched off earlier. He ruled out any relationship to the arachnids on the basis of what he called the seventh pair of appendages not being present.

By the time he wrote his monograph a great deal more information about the pycnogonids was available. Also he had repudiated his recapitulationist views on the nauplius and the zoea. He provided detailed anatomical and systematic descriptions of the animals, and attempted a provisional classification. His monograph was the basis for all subsequent work (Helfer and Schlottke, 1935) on a group that continues to frustrate efforts to develop a satisfactory phylogenetic arrangement or even come up with a good tree (see Hedgpeth, 1947, 1954; Fry, 1978). Dohrn agreed that the pycnogonids, like other arthropods, are modified annelids, and on the basis of this comparison he had some insights concerning the common ancestor of the group. It would have had a series of relatively undifferentiated metameres with limbs or modified limbs. Genital openings on several of these were part of that homogeneity and indicated an early divergence of the pycnogonids from their closest extant relatives. The animals were highly modified at both ands of the body. At the front end there was a suctorial feeding apparatus that had no obvious homologue in any other arthropod. At the posterior, there had been much reduction, with loss of many segments and no abdomen persisting as a distinct body region. Various organs such as the gonads had been displaced into the legs.

Dohrn's treatment of the larvae and the «extra» pair of appendages was affected by recent advances in the reproductive biology of the group. Pycnogonids, as a general rule, feed suctorially with their modified proboscis, and might be considered a kind of ectoparasite. Pycnogonid larvae, unlike those of marine crustaceans and, indeed, unlike the generality of marine invertebrates, are not motile creatures that disperse and settle at a suitable habitat. Rather they are not motile at all, but are transported by their parent. Interestingly enough, it is not the mother, but the father, who cares for the young. This had come as something of a surprise, but, as Dohrn realized, there are other animals in which the father cares for

the young but the mother does not, such as sea-horses and their relatives. The eggs are transferred to his body, where they develop, and he delivers them to the appropriate place. The «extra» limbs («ovigers») are present in all male pycnogonids with the sole known exception of one species of the genus *Pycnogonum* and in the females in some species. It is now known that the father produces a kind of cement, and that the ovigers process this so as to hold the young together. Dohrn thought that the ovigers of females are strictly vestigial, and indicated that both parents had previously cared for the young (page 93). As it turns out, the ovigers are also used by some pycnogonids in cleaning the body, so an alternative scenario becomes available, one with a *Funktionswechsel* in which the main function was cleaning and the subsidiary function of parental care evolved in males and the organ itself was lost in many females.

Dohrn rejected the notion of Semper (1874) that the ovigers were a «new formation» on the grounds that the animals would initially have had to carry the eggs on limbs that did not yet exist (p. 92), and compared new formations in general to special creations. He preferred to consider the mouthparts and ovigers as having been produced through *Funktionswechsel* from limbs. A Darwinian approach is capable of accounting for the origin of new parts and features, but only with difficulty, whereas reductions and secondary losses are a matter of routine. So it stands to reason that Dohrn would want to have the ovigers be a primitive feature rather than a secondary acquisition, and would accept the consequences of that, including an early divergence of the pycnogonid lineage.

Manton (1978) insists that the pycnogonids have indeed added a limb at this point, on the grounds of similarities in locomotory functional anatomy between pycnogonids and arachnids. She made this seem more plausible on the grounds that within the group there are a few isolated cases of secondary increases in the number of appendages, though these are morphologically similar to the posterior appendages. The general rule in arthropods is that the number of segments has become gradually more stable beginning at the front end and proceeding toward the rear. Adding a segment at the front end is still implausible, and given a modest amount of convergence and parallelism, plus some conflicting evidence, a somewhat earlier derivation of the pycnogonids without recourse to such an addition remains a very reasonable interpretation. But even if that intercalation has in fact occurred, it is simply an unusual exception to a generally valid rule, not grounds for rejecting the rule altogether.

Given a model of a hypothetical ancestral pycnogonid, Dohrn was in a good position to do some cladistics with a functional aspect. He could polarize the characters on the basis of his model, and also justify the direction on the basis of adaptive significance. He thought that the group was relatively homogeneous, and therefore decided not to subdivide it into taxa of high rank. There had been a modest adaptive radiation with some diversification in feeding habits and way of life. At least for some characters it was a relatively straight-forward matter to decide which conditions were primitive and which derived. The whole group showed a trend from ovigers being present in both sexes, to ovigers being present in just the males. The first appendage began with a well developed pincer, then had a rudimentary one, or the appendage was lost altogether. The second appendages also might be lost. The number of genital openings declined from three pairs to two, and finally to just one pair. I mention only some of these trends.

There was a crude correlation between these modifications, so that the genera *Pycnogonum* and *Rhynchothorax*, united in the family Pycnogonidae, shared a number of them. The functional reason for reduction of limbs was thought to be that the suctorial apparatus had become the main organ of feeding and accessory mouthparts were no longer necessary. But given that these changes all go in one direction, they are apt to give rise to a gradal classification — one that simply ranks animals according to whether they are relatively primitive or advanced. They are the sort of innovations that are apt to be subject to parallel evolution, just like the opisthobranch gastropods that evolve polyphyletically from snails into slugs (Ghiselin, 1966; Gosliner and Ghiselin, 1984). Under such conditions one needs derived characters that are also divergent if the result is to be clades rather than grades. It is therefore not surprising that Dohrn himself expressed dissatisfaction with his system, and that subsequent workers have been likewise disappointed.

Dohrn and his employees and supporters pushed on with research on the «lower» vertebrates, especially sharks, in order to develop his ideas about vertebrate origins. The *Mittheilungen* of the Station, its house organ, devotes many publications to his project. Although he failed to justify the annelid theory, Dohrn did make important contributions to comparative vertebrate anatomy, thanks especially to his work on the embrology of sharks. I will not go into the details at this time, but should mention that a detailed acount of his work has been presented by Kühn (1950). Rather it is important that we note Dohrn's influence upon the Russian school of evolutionary morphology, especially its founder, A. N. Sewertzoff (1866-1936) (see Ghiselin, 1980). Sewertzoff and his successor Schmalhausen freely and openly acknowledged Dohrn's contribution. The *Ursprung* was treated as canonical literature, and Schmalhausen (1937) wrote a long and appreciative introduction to the Russian translation.

Sewertzoff visited the Station in 1897, in order to study the embryology of fish, including teleosts, selachians and cyclostomes. Sewertzoff (1899) was obviously working on the same kind of problems that interested Dohrn, but the influence of Dohrn upon Sewertzoff is not immediately apparent. It was only much later that Sewertzoff (1927, 1928, 1931) brought the work of Dohrn and others on *Funktionswechsel* and related topics up to date. Sewertzoff (1931) also wrote one of the best discussions on the relationships between ontogeny and phylogeny. He stressed the point that recapitulation occurs in a straight-forward manner only when there has been terminal addition. Sewertzoff (1931: 248) expresses regret that in his earlier works (Sewertzoff 1912, 1928) he had overlooked how Fritz Müller (1864) had presented early divergence as an alternative to terminal addition. He accuses Darwin, along with Haeckel and Weisman, of not having appreciated that point. And yet, as we have seen, Darwin was Müller's source on that very

point! If Sewertzoff did not do proper justice to Darwin, and if his mature appreciation of Müller was at least in part a sort of rediscovery, then it seems likely that the Russian endorsement of Dohrn was at least partly retrospective as well.

Manton (1977) presents the functional approach as someting that was invented by H. Graham Cannon, which may have been true of her own functional approach, hardly does justice to biology in general. I find that although Manton (1977, 1978) cites Dohrn's monograph on the pycnogonids, she does so only with reference to the illustrations, not the text, and that may explain the oversight. This is, of course, no isolated incident. Systematists, like other scientists, work within a very narrow disciplinary context. They all too often overlook the accomplishments of those who specialize on taxonomic groups other than their own, neglect the older literature and that in foreign languages, and quite generally stick to tradition and routine.

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Some concepts of historical science

«The nourishing fruit of the historically understood contains time as a precious but tasteless seed.» - Walter Benjamin

Abstract – The goal of this paper is to explore the concept of historical science, Many analysts of science distinguish between historical and ahistorical sciences to argue that some practices are more «scientific» than others, that the distinction supports a particular view of proper scientific method, or that some are mere pseudo-sciences. After discussing these reasons for calling a science historical, six different analyses of the concept of historical theory or science are discussed. I conclude in favor of a pragmatic view, drawing on Danto's analysis of narrative, in which a science is historical to the extent that it admits narrative as contributing to understanding.

The goal of this paper is to explore the concept of historical science. It is claimed that evolutionary theory and the biological sciences that use and develop it, e.g. systematics, are historical sciences. Such a claim is sometimes used to differentiate among sciences, e.g. to classify them as «hard» or «soft». Since many authors discussing the nature of systematic biology, theory, or practice assume a clear distinction between historical and ahistorical, it is helpful to examine several such concepts. The approach used here is philosophical: examining proposed distinctions between historical and ahistorical sciences (or theories) and criticizing them for failing to distinguish among sciences (or theories) that common intuition distinguishes. Since the aim in making such distinctions is either to aid understanding of the nature of the sciences or to make value judgments (e.g. to set priorities for funding or ranking for prestige), the philosophical exercise has practical merit. The aim is not, however, to criticize claims in the philosophical and biological literature in order to establish which philosophical «school of thought» has the correct analysis of science. Rather, the practical merit in the philosophical exercise is to defend the intellectual autonomy of systematics against the criticisms of theoretical and sociological reductionists.

Why call a science historical?

Three reasons one might call a science historical are to argue that: (1) a science, for being historical, is no less legitimate or valuable than other, ahistorical sciences; (2) a certain model of explanation that serves as a standard of scientific acceptability, e.g. Hempel's deductive-nomological or covering-law model, applies to the science even though nothing like Hempel's ideal schema appears in the main texts of the practitioners; (3) the kind of warrant, or justification, of knowledge or understanding claims is distinct from that of ahistorical science. Three more reasons just negate the first three: (1′) in being historical, a science is distinctly illegitimate, unfounded, or at least inferior to ahistorical science; (2′) If Hempel's covering-law model of explanation (or something like it) does not apply to a subject, that subject is not a science at all; (3′) The kind of warrant or justification in historical science in the same as for ahistorical science, and therefore the knowledge produced by historical science is weaker because the warrant is generally less for its claims.

I will consider these reasons before discussing six conceptions of what makes a science historical because they color one's reading of the concept of «historicality». The different concepts suit different purposes, and it is not at all clear which reasons and concepts should be judged compatible. I shall not consider the compabilities in detail, but only review four concepts and offer two more.

Positive and negative reasons are considered together because I do not aim to endorse arguments committed to one side or the other. Scientists engaging in turf battles for legitimation, authority, domination, money, power, students, laboratory space, or glory, often invoke the legitimacy reason in arguments to secure places in a «pecking order» for different sciences or to reject hierarchies of authority and social status altogether. The others are more typically used by historians or philosophers concerned to formulate general principles of science or methodological principles for their own disciplines.

Typically, authority hierarchists place physics and other physical science at the top. Then comes biology and the «historical» parts of geology and other earth sciences, then psychology, and then the lowly social sciences like sociology and anthropology. Equally typically, anti-hierarchists argue for some sort of «pluralism», with all sciences on an equal footing. For example, in «A plea for the high status of natural history», Stephen Jay Gould (1989, 280-81) takes Nobel laureate physicist Louis Alvarez to task for likening paleontologists to stamp collectors and calling them «not very good scientists». Gould defends the autonomy and authorithy of natural histo-

ry by invoking the power of historical interpretation on the one hand and the ignorance of physicists about natural history on the other.

The second reason, regarding the nature of scientific explanation, typically concerns philosophers of history, whose project this century was transformed by Hempel's 1942 essay, «The Function of General Laws in History». This essay set the stage for his controversial covering-law model of explanation (Hempel and Oppenheim 1948; Salmon 1989) and capped two decades of disputation about whether history was a scientific discipline or could be reduced to one.

Along with a number of other developments in the philosophy of empiricism that grew out of the logical positivism of the 1920s, Hempel's work polarized general discussion about science around the issue of the reducibility of the central theories of one science to those of another. The reduction debate was driven by three features of Hempel's conception of explanation: (1) that, ideally, explanations are sound deductive arguments from premises including statements of general laws of nature and particular conditions about the phenomenon to be explained; (2) that explanation is the core project of any science; and (3) that since deduction allows the explanation *of a law* by more general or «logically powerful» ones, the laws of one science might be explained by those of another, more powerful science. This last feature provides the basis for a conception of the growth of scientific knowledge as the reduction of less powerful theories to more powerful ones.

When philosophers turned their attention to sciences like geology, systematics, and evolutionary biology, it proved difficult to formalize the relevant theories along deductive lines (Flew 1959, Smart 1963, Williams 1970). The expectation of success was formed largely through the tacit inductive argument that if a few select physical laws of mechanics can be so formulated, then all of physics can and, by appeal to principles of hierarchy and reduction, then all of science can.

Some of the qualities that made formalization of the «soft sciences» difficult align these sciences with the humanities and social sciences rather than with the physical sciences, Goudge (1958), for example, defended such an alignment, arguing that explanations in natural history have more the structure of coherent narratives than of deductive systems. Despite this, such narratives could be causal explanations. Therefore, according to Goudge, the philosophical model of deductive arrangement under general causal laws, which is lacking in natural history narratives, cannot lay exclusive claim to causal explanation. Nor, therefore, can physics lay claim to a scientific method superior to that of the «historical» sciences (Goudge 1958, 202).

The narrative quality of Darwin's adaptive explanations is manifest in the structure of this argument for evolution and natural selection (e.g. Beer 1985; Gould 1986). This «literary» quality looked problematic to those logicians who rejected as meaningless all statements lacking means of empirical verification. They accordingly tried to explain Darwin's theory away (e.g. Nagel 1961 for teleological explanation in general), or to argue that such sciences are inferior science or even pseudo-science (e.g. Popper 1957, who later changed his mind about natural selection, see Popper 1972, 1978). Smart (1963) argued that since there are no general laws for particular species, evolutionary biology was not scientific. This statement helped provoked the elaboration of the philosophical analysis of species as individuals rather than kinds or classes (Ghiselin 1974, Hull 1980). The species-as-individuals view supports an argument that there should not be laws about particular species and that philosophers and others misjudged evolutionary theory in claiming it had no laws and was unscientific. Rather, they had been looking in the wrong place for laws.

Calling a science historical because it fails to reduce to physics is a reason I will not explore further. I do not believe explanation, as laid out by the Hempelian tradition, is necessarily the central project of a science, nor do I believe that there is necessarily any such beast as the «core theory» of a science in Hempel's terms. My reasons trace to suspicions of vagueness and ambiguity in the concept of «theory» and the likelihood that holding such concepts in high regard will lead to error, or worse.

Although the analytical philosophy of history (Danto 1985) has done much to widen the scope of general philosophical discussion on the topic of explanation, the latter's ultimate purpose is too narrowly epistemological to serve my goals. Philosophical theories of explanation distinguish too rigidly between «discovery» and «justification». This once useful distinction now serves only to insulate deductive inference from the scrutiny that other aspects of scientific practice routinely receive by historians and sociologists as well as philosophers of science. The question of what justifies deduction itself is part of the general problem of justification. Deduction has become a self-justifying (or unjustifiable) axiom for philosophy of science. And this in turn has masked the important fact that logical empiricist philosophers of science are themselves merely using a bit of predicate calculus as off-the-shelf technology. There is no *a priori* reason one could not or should not take narrative as an alternative basis for science.

Justification or warrant concerns the relation between evidence and hypothesis, while explanation concerns the relation between premises in an explanatory argument and conclusions, or between questions and answers (van Fraassen 1980). Thus, regardless of what purposes are served by invoking scientific legitimacy or the pattern of explanation, a third reason to call a science historical is that it differs in the style of justification from ahistorical sciences. That is, its evidence bears a different relation to its hypotheses. Advocates and critics of the distinction between historical and ahistorical science can agree that producing an explanation and justifying it are logically distinct operations, and yet disagree on whether the distinction between styles or types of justification, and therefore between different kinds of science, serves any important purpose.

Claims about warrant (reason three) are sometimes linked to the first reason through an argument that, because science becomes unified by a *universal* logic of warrant, a science is legitimate to the extent that it satisfies that logic. Scientists sometimes defend a particular science against the charge that it is inferior or pseudo-science by arguing for the epistemological unity of science (and against a distinction between historical and ahistorical science). But

scientists sharing the goal of defending the legitimacy of particular sciences can fall on either side of the unity of science question. One can analyze history itself in such a way that it is scientific, and therefore that historical sciences are scientific, or one can deny that being historical entails not being scientific on grounds other than warrant and thus still accept epistemological unity. On the other hand, one can reject epistemological unity as a goal of science and then nothing is entailed about whether a practice is scientific just in virtue of being historical. Therefore, neither commitment — to unity or disunity — is effective in defending a science against its critics.

Historians and philosophers of science also pursue common legitimation goals with different commitments to epistemological unity or disunity. Some recent essays from a symposium on evolution as a historical science illustrate this. Richards (1992) relies on the distinction between historical and ahistorical science, but to argue *against* the Hempel model as a basis for unity. Richards argues that Hempel's model gets the nature of explanation backwards. Hempel did not claim that acceptable explanations in actual scientific practice meet the formal conditions he defined. Rather, he offered them as an explanatory ideal to which real explanations are better or worse approximations. Real explanations might not meet the ideal by failing to explicitly mention laws, although these might be supplied by post hoc historical or philosophical analysis in particular cases. Hempel called such approximations «explanation sketches» that could in principle be filled in. Many commentators have taken Hempel's idealism to insulate his model from the criticism that it failed to account for actual scientific explanatory practices. Richards argues instead that historical narrative explanations — far from being mere explanation sketches — are the ideal, and that deductive-nomological explanations (even those meeting all of Hempel's requirements) are mere *narrative* sketches. Unity of science is preserved by standing the logic of explanation on its head.

Hull (1992) likewise relies on the historical/ahistorical distinction and likewise argues against the emphasis on laws in the Hempel model, but on different grounds than Richards. Hull defends a «particular-circumstance» model of explanation against Hempel's covering-law model to capture the sense that, even within the broad framework of deductive inference, in historical sciences the conditions or particular circumstances rather than the laws govern the character of explanations. Thus, while Richards defends epistemological unity of science by arguing that narrative rather than deduction unifies explanation, Hull defends plurality of explanatory practice within a broad epistemological unity of deductive form.

Ereshefsky (1992) does something orthogonal to both Richards and Hull. He rejects the historical/ahistorical distinction among forms of explanation and considers the Hempel model a useful (though perhaps limited) paradigm. He argues instead that evolutionary theory *is* historical, but because some of its central entities — taxa — are a special type of historical entity, not because its explanations are historical in form. Hull argues that the model of *explanation* in evolutionary theory takes a distinctive, particularistic form because the entities are historical, thus accepting the classical basis for the historical/ahistorical distinction in the form of explanation. Ereshefsky rejects the classical basis, but accepts a new distinction based on the nature of the entities rather than the form of explanation. He argues that this new distinction is compatible with the Hempel model *and* the Ghiselin-Hull philosophy of historical individuals.

Laudan (1992) rejects the distinction between historical and ahistorical science, not because she sees an alternative route to challenge Hempel's analysis of the form of «proper» scientific explanation (Richards, Hull) or because the entities of some sciences are historical entities (Ereshefsky), but because she rejects the question of explanatory form as the significant one. She suggests that philosophers of history should look again at the literature on scientific explanation (i.e., they should bring their history of philosophy up to date). They would find that in the fifty years since Hempel proposed his model, it has ceased to be the only viable formal model, and is no longer the most promising one to many philosophers.

Laudan takes the difference between sciences like geology and biology on the one hand and physics and chemistry on the other to be a *scientific* question about warrant, not a philosophical question about the logical form of explanation. The scientific problem is to devise means of acquiring reliable knowledge. She traces the motivation to distinguish historical from ahistorical science to «observational difficulties» about reconstructing the record of the past and argues that the gradient of difficulty in this regard among the sciences does not make for epistemological disunity, whatever form explanations in different sciences may take (Laudan 1992, 62). The fact that a laboratory physicist or geneticist has less trouble reconstructing the history of events in their experimental set-up than does a field paleontologist tracing a fossil record or a systematist reconstructing a phylogeny does not make for a difference in kind, but only in degree. Solution to the problem of stating the general terms of scientific warrant does not imply anything, therefore, about the epistemic unity or disunity of the sciences.

The objective of Laudan's argument is to deny an appeal to the complexity of geological processes and incompleteness of the data to sustain a distinction between historical and ahistorical science. Danto (1985, 340) argues the same point in a more general context: incompleteness of record is a «banal and contingent» fact about historical data, not what makes a practice historical. We shall see below why appeals to complexity and incompleteness fail to ground the distinction.

As far as devising means of acquiring reliable knowledge goes, the issue of narrative vs. deductive form of explanations is tangential to the epistemological problem of warrant (Laudan 1992, 64). The only historical/ahistorical distinction Laudan admits is that narrative explanation requires an additional justification step: connecting parts of chronologies using particular causal theories. The link between use of causal theories and parts of chronologies is important for characterizing historical science, but a proper analysis would show that the distinction can be drawn independently of arguments for or against epistemological unity (Griesemer ms).

One may doubt that arguments pursuing any of the three reasons for calling a science historical can be effective on the grounds proposed. One can argue for or against legitimacy, explanatoriness, or warrantability of a science while accepting or rejecting the claim that it is distinctively historical and while accepting or rejecting the claim that the sciences as a whole are epistemically unified or disunified. Pushing further, I will argue that what makes a science historical is a pragmatic matter of taste rather than logic, and the distinction is one of aesthetics and judgment. Put differently, questions of logical form are distinct from questions of logical relation and questions of historical form are distinct from questions of historical relation. That explanatory form and historicality are pragmatic matters in no way forces one to take up sides on the largely sterile controversies dividing relativists and realists or objectivists and subjectivists.

What is a historical science?

I will not discuss all the concepts needed to interpret the claim that some sciences are historical and others not. Concepts like «chronicle» and «narrative» are mentioned only to introduce an alternative view of what makes a science historical. Danto (1985) analyzes the relevant concepts.

A good start in answer to the question is made in Wright, Levine and Sober (1992). In a section authored by Sober and titled, «The Historical Character of Evolutionary Theory» (48-51), four concepts of the historicality of historical science are discussed (cf. Levine and Sober 1985).

The first conception is one that Sober dismisses as trivial, failing even to demarcate evolutionary theory from «billiard ball» mechanics. Even though I will ultimately distinguish «historical science» from «historical theory», the claims to follow are worth considering irrespective of whether science or theory was the author's intended target.

1. A theory is historical if the statements it explains refer to two or more moments of time

This is trivial because any science that deals with temporally extended entities, events, or sequences must refer to multiple moments in time. Time here is the tastless seed, not the nourishing fruit. The fact that billiard ball mechanics refers to the states of balls at different times suffices to classify it as historical according to criterion 1. Indeed, it is hard to see how theories of any physical processes could to otherwise, and since evolutionary theory is a theory of certain physical processes, claim 1 does not demarcate evolutionary theory from any other dealing with physical processes, nor any science based on facts of natural history from other sciences. And even if systematics is interpreted as a theory of certain temporal relations or patterns among taxa rather than processes, it would not be distinguished from a similarly interpreted physics, e.g. one interpreted in terms of functional relations rather than causes (e.g. Russell 1913).

It does not follow, however, that claim 1 does no demarcation work at all. It demarcates the sciences of pure abstractions — «Platonic objects of thought» — such as mathematics and philosophy from empirical sciences of the physical world. Abstract objects are not in time, and therefore their explanations do not require reference to moments of time.

A more promising thesis is one that Sober characterizes as attributing «the Markov property» to a scientific theory. Sober (Wright et al. 1992, 48) traces this view to Gustav Bergmann and quotes an adaptation of it by Hull (1974).

2. A theory is historical when «knowledge of the past is *necessary* to predict the future. Knowledge of the present alone will not do»

It is important not to overinterpret claim 2. It does not assert that knowledge of the past is *sufficient* to predict the future, but only that it is *necessary*. If real physical systems exhibit chaotic dynamics, then even very precise information about the past may be insufficient to predict the future (My thanks to Professor Scudo for raising this point). Claim 2 does not claim so much, but Sober rejects it on several grounds. First, he points out that in population genetics, standard models require only the gene and genotype frequencies of the population at a given time plus a specification of the evolutionary forces in play *at that time*. If population genetics is taken to be the core of evolutionary theory, and one claims that evolutionary theory is historical, then Sober's point has some merit: since population genetics does not (or at least need not) have the Markov property, evolutionary theory is not historical by criterion 2. One may, of course, deny that population genetics is the core of evolutionary theory or conclude that evolutionary theory is not historical without doing serious damage to claim 2.

Sober makes a more important second point about references to the past: any dynamical theory will *in practice* typically require knowledge of the past as well as of the present to predict the future. In order to predict without reference to the past, a theory must be dynamically and empirically sufficient relative to the choice of state variables, parameters, and state space (Lewontin 1974, Wimsatt 1980, Lloyd 1988). Otherwise, our poor knowledge of how forces combine to produce effects will require that to predict we must know things about the temporal order in which the forces operated in the past. Cartwright (1983) makes the same point when she argues that mechanics is the only example of a dynamical theory for which there is a general rule (vector addition) about how to combine forces. She argues that, more typically, the lack of general laws of interaction leads to the complex form of «phenomenological laws» used to predict in practice. These are distinct from the pristine «fundamental laws» used to explain. For a theory like evolutionary theory, one needs in addition a lot of variables and a lot of care in their measurement to avoid empirical insufficiency, which is also required to predict a future state of an evolving system from its present state alone.

Indeed, for evolutionary theory, Lewontin (1974) suggests that we will rarely meet conditions of dynamical and empirical sufficiency to make interesting predictions about evolutionary systems in nature. But this failure in practice does not lead Sober to

argue that evolutionary theory is historical. He instead argues against the interpretation that flows from claim 2. It does not follow that a theory is historical merely due to failure to meet the practical requirements of dynamical and empirical sufficiency. In practice, one can sometimes substitute a knowledge of history for satisfaction of formal sufficiency. But it would be a mistake to confuse this empirical and contingent fact with a conceptually necessary property of historical science.

While I accept Sober's point about theories, and therefore his conclusion that claim 2 fails to demarcate evolutionary theory from others in the class of dynamical theories, there are caveats. It is not clear how far Sober's conclusion about a rather unspecified evolutionary theory carries to other theories and theoretical structures in evolutionary biology, e.g. to theories of speciation, or more importantly to the collection of methods and assumptions that play a role in systematics practices such as cladistic analysis and phylogeny reconstruction. Sober (1988) argues for the dependency of cladistic inference on model assumptions about the evolutionary process, but that does not suffice to show that cladistic practice depends on any particular version of evolutionary theory. Therefore, the failure of claim 2 to establish the historical nature of evolutionary theory does not imply that systematics is also ahistorical.

Caution must be exercised in two ways in evaluating these arguments. One is in articulating the content and structure of theories. If theories are best presented through models rather than axiomatized laws, it may turn out that what can be done with models in practice plays a more important role that any conceptually necessary claim about the historical or ahistorical nature of the theory, making precise statement of the latter irrelevant to understanding what it means to say that the theory is historical. Second, we may be forced to distinguish between theories and sciences if practice is relevant. A *science* in which a theory is constructed and used to make predictions may be historical even if the *theory* itself fails the test of claim 2. (It should already be clear that in calling a science historical, I am not concerned with the idea that all sciences are historical because they *are* practices and that all practices are historical).

Distinguishing between a science and a theory leads to the further concern that we are perhaps being overly respectful of the idea that prediction, like explanation, is a relation between premises and conclusions of arguments. The covering law model of explanation (and by Hempel's symmetry thesis, prediction) not only leads us to think of prediction in this way, but also leads to inattention to the practice of argumentation. Hempel was sensitive to this in his claim to be formulating idealized concepts of explanation and prediction, not analyzing or criticizing actual scientific explanations. The latter amount to mere explanation sketches in Hempel's analysis. But they are none the less powerful for failing to meet the ideal, and if the idealization is so stringent that it is never met in scientific practice, then practice, not the ideal, should be the focus of attention in trying to understand what makes a *science* historical. To the extent that explanatory and predictive practice falls outside the bounds of what is typically called «theory», we may need to distinguish claims about historical science from claims of historical theories so as to fix the meaning of what is necessary to predict the future.

So, the need for too many variables in practice to achieve formal sufficiency (the heart of claim 2) does not work well as the basis of a criterion of demarcation among the sciences. We would have to know a lot more about the relation between formal structure and practical use of theories than is evident from the literature on theory structure to make claim 2 work.

Another criterion moves from claim 2's generic appeal to knowledge necessary to predict, to a more specific appeal which Sober identifies (in philosophy of evolutionary biology) with Morton Beckner (1959).

3. A theory is historical when it contains at least one historical concept

Sober suggests that Beckner's chosen example, that physiological theory is historical because it contains concepts of physiological states that are historical, such as «hungry», is inapt. Physiologists are quite comfortable explaining physiological processes with methods drawn from physics and chemistry that (by assumption) do not require any historical concepts. To understand «hungry» as a historical concept one would therefore be thrown back on a version of claim 2, that a theory contains historical concepts because they are the means used to refer to the past, which is necessary to predict the future. But Sober offers another, better example: «adaptation». The now standard reading of (evolutionary) adaptation is that it applies only to traits that have arisen by a «historical process» of natural selection. That is to say, present states of adaptedness are outcomes of natural selection processes that operated in the past.

But Sober rejects claim 3 as well because it implies that many concepts from physics, e.g. acceleration, are also historical and therefore that physics is a historical science. He further points out that the process laws of evolutionary theory, such as concern the principle of natural selection, are ahistorical in the sense of claims 2 and 3, so it is hard to see how appeals to claim 3 can succeed merely by application to concepts regarding the outcome of such processes.

Perhaps the main difficulty with claim 3 is also the reason for the faint hope that it could work. It merely pushes the problem of historicality of theories back to the problem of historicality of concepts. If a criterion of the latter could be produced independently of any assumed meaning of the historicality of theories, then claim 3 might succeed. Sober's argument against claim 3 simply shows that we have not succeeded in an independent characterization, not that claim 3 fails. Appeal to the historicality of «adaptation» as a concept depends on the assumption that the process of natural selection is historical, perhaps just in virtue of being a process. While that may in fact be true, it fails as a demarcation criterion since it throws us back on claim 2 or claim 1, both of which fail, as we have seen. Unfortunately, I have no further insight on how to characterize «historical concept» independently, so I reject claim 3 as unpromising but not conclusively false.

Finally, we reach Sober's preferred criterion:

4. A theory is historical if it «has a built-in temporal asymmetry. The theory enshrines a difference between the direction from present to future and the direction from present to past»

Sober recognizes that this claim fails to demarcate evolutionary theory from all of physics. Thermodynamics turns out to be a historical science according to claim 4 through its formulation of the principle of entropy. To suggest that this demarcation failure is acceptable, Sober notes the deep parallel between evolutionary theory and thermodynamics that R. A. Fisher developed in his fundamental theorem of natural selection. Fisher (1930) argued that selection causes an increase in mean population fitness in proportion to the additive genetic variance in fitness. Sober, of course, must take care of the objection than mean population fitness need not be maximized by natural selection (e.g., if it is frequency-dependent). Professor Scudo (pers. comm.) points out that Fisher's fundamental theorem is not true in general, but the point here is not about its truth, but about the parallel to principles in physics. Since the same *sort* of caveat is true of increase in entropy, these objections do not undercut the comparison between biology and physics. And in accepting claim 4 as adequate, Sober acknowledges that some parts of physics are historical.

Once again, a question about practice arises. The highly mathematized, clearly formulated evolutionary theory of which Sober speaks is tethered at very few points to data about natural populations. In fact it is most successful only in highly constrained laboratory populations and abstract mathematical models. True, claim 4 works as a criterion applied to this idealized, abstracted theory and I am willing to accept it as such. But it teaches us little about evolutionary theory or evolutionary science to call an abstract model historical. Moreover, if natural selection in nature is almost always frequency-dependent, then analysis of the theory has only a tenuous grip on the practices of evolutionary biologists trying to understand evolution in nature. This not to say that the theory is not a triumph, but only that the worries raised above are still in play. Moreover, the theory is only remotely connected to the practice of systematics, and most definitely not connected to cladistic or phylogenetic patterns through successful, precise predictions. So judgment on the basis of acceptance of claim 4 that evolution is a historical science rests on the still unjustified claim that the mathematical theory of evolutionary genetics is the «core» of evolutionary theory.

Worse still, as I noted above, it is not clear that systematics *has* a central theory in the way that evolutionary genetics does, though I would certainly agree with Ghiselin (1969) that Darwin's theory of descent with modification and his principle of natural selection are core if anything is. My worry here is with the concept of «core», not of «theory» — we don't have a thorough understanding of the relation between theory and practice to justify the linkage required to sustain claim 4 as an analysis of historical science. My point is that a demarcation criterion like claim 4 may never be directly applicable to a science like systematics unless its application to the core *theory* helps us interpret systematics practices as well. Such help may eventually be produced, but the indirect application of claim 4 solely through the rhetoric of evolutionary synthesis and core looks rather dubious.

One thing claim 4 has going for it is a certain similarity to views expressed by Stephen Jay Gould (Gould, Gilinsky & German 1987). Gould argues, going back to the heyday of «nomothetic paleontology» and random clade studies by the «MBL Group», that the data of clade diversity show historical directionality. Gould et al. argue that clades that originate early in the history of a larger group tend to be bottom-heavy, i.e. to have more members in the first half of their temporal duration than in the second half. (Put differently, that their «centers of gravity» are at less than half their duration, measured by first and last appearance in the fossil record). Clades that originate late in the history of a given larger group tend to be «neutrally bouyant» or top-heavy. Thus the history of a larger group has a signature in the statistics of clade shape at any given time-plane. Thus the data themselves show directionality.

If there were a theory of clade diversity that explained the phenomenon discussed by Gould et al., then it would probably be a theory which satisfies claim 4 and would therefore be a historical theory. I do not think that such a theory currently exists. But more importantly there is some ambiguity in claim 4. The first sentence of the claim requires that «it», the theory, has the built-in tenporal asymmetry. But since theories are abstract objects (on the usual philosopher's reading, which is tacit in the covering-law model of explanation), it is ambiguous to say that *the theory* has a temporal asymmetry built-in. Presumably this is clarified in the gloss in the second sentence: the theory «enshrines» a difference in two temporal directions, i.e. the theory describes or entails an asymmetry in nature. But the second sentence is also ambiguous. It either means that the theory refers to a temporal asymmetry in the phenomena, or that it makes some claim or assumption about the nature of time itself. If we assume the former, then claim 4 seems to be in line with the empirical claim of Gould et al. The data shows directionality, so a proper theory of clade diversity, if we had one, would satisfy claim 4.

But now we are left with a troubling counterfactual application of claim 4 to a *science* in order to argue that a *theory* is historical: if the data of a science have a built-in temporal asymmetry, and if there were a proper theory for such data, then the theory would be historical. This is clearly inadequate, because it does not follow from the temporal asymmetry of the data that *every* theory of them would satisfy claim 4, and how are we to distinguish counterfactually the ones that are historical from the ones that are not? What pressure is there from nature on our scientific interests, such that we formulate a theory historically so as to «mirror» this aspect of the phenomena? Mirroring nature is something scientists may or may not wish to do with their theories.

In the light of this lack of a proper theory of clade diversity, and of a meta-theory sufficient to infer that a proper theory of clade-diversity would meet claim 4, one might be tempted simply to cut theory out of the picture by altering claim 4:

4*. If the data have a built-in temporal asymmetry, then the *science* that includes those data is historical

But claim 4* is suspect as well. Thus far we have only seen difficulties in extending criteria of demarcation for historical vs. ahistorical theories to sciences. By switching to the data of a science from the nature of a theory, we no longer have conceptual resources enough to judge whether claim 4* is satisfied. Why, for example, couldn't we adopt Sober's criticism of claim 1 along with the theory that time is asymmetrical to argue that all sciences of the physical world are historical? Then every pair of data points referring to distinct moments of time will exhibit temporal asymmetry: one datum is earlier than the other. We do not require some *further* «signature» in the data to know that data necessarily exhibit temporal asymmetry of this fundamental sort. Indeed, the very idea of data from different moments in time implies temporal asymmetry. But if we want to rule out the temporal asymmetry of time itself as the relation through which data are considered to satisfy 4*, how can a restriction be made? What makes one asymmetric relation relevant and another not? What makes a theory or a science historical, in short, is not the nature of the data, but what scientists do with them.

Thus, I conclude that the four options discussed by Sober et al. are not satisfactory. Let me add two more: one that, like the others, is unsatisfactory on conceptual grounds but nevertheless interesting because it results from considerations of problems fundamental to systematic biology, and another that does the work I want it to, though it will probably not satisfy philosophers as a respectable criterion.

Philip Kitcher (1989) revisits the question whether species are individuals or classes (sets) from the point of view of formal logical issues. Kitcher offers a criticism of the species-as-individuals view that leads to an interesting possibility for a criterion of what makes a science historical. Kitcher does not develop such a criterion per se, nor is that an aim of his essay and critique of the Ghiselin-Hull species-as-individuals theory.

In criticizing the species-as-individuals theory, Kitcher tries to disentangle what he sees as a confused and misleading claim, that it is a thesis about the ontology of species, from what he sees as an interesting thesis about what makes individuals historical. Since species-as-individuals theory entails that species are historical individuals, Kitcher expects it to formulate a position on historicality. I will use Kitcher's formulation of such a position below to state a criterion of historicality for a science.

Kitcher introduces a concept he calls «historical connectedness» in order to say what he thinks is at the heart of the answer to the interesting problem posed by the Ghiselin-Hull theory. He offers two formulations, one in the idiom of mereology (the logic of parts and wholes or individuals), and one in the idiom of set theory (the logic of members and sets). Kitches draws on two alternative logical schemes because he thinks that Hull's arguments do not suffice to show that species are not sets. This does not mean that Kitcher has shown that species *are* sets, but only that he thinks Hull has not shown that they are not. By offering a formulation in terms of mereology and one in terms of set theory – logical schemes with different ontological assumptions – Kitcher maintains neutrality on whether the Ghiselin-Hull theory is about the ontology of species.

The mereological version of Kitcher's criterion of historical connectedness is as follows:

> ... we conceive of an individual with organisms as parts to be historically connected just in case for any organismal parts x and y such that x preceeds y and for any organism z, if z belongs to a population that descended from a population containing x and that is ancestral to a population containing y then z is also part of the same individual as x and y. (Kitcher 1989, 187).

The set-theoretical version is:

> A set of organisms is historically connected just in case it satisfies the following condition: for any organisms x, y and z, if x and y are in the set and if z belongs to a population that is descendant from a population which has x as a member and that is ancestral to a population that has y as a member then z is in the set. (ibid.).

Kitcher goes on to develop an interesting argument for the claim that if the Ghiselin-Hull theory that species are historical individuals means that species are historically connected entities, then their theory is incompatible with Mayr's biological species concept. Kitcher argues that the biological species concept is compatible with species not being historically connected, and since his formulation of the Ghiselin-Hull theory implies that species must be historically connected, there is a contradiction.

While I do not think the argument is sound, an interesting criterion for what makes a theory or a science historical can be constructed using Kitcher's criterion of historical connectedness:

5a. An entity is historical if and only if it is historically connected

5b. A theory (or science) is historical if at leastsome of its objects are historical entities

Unfortunately, there is an equivocation on the meaning of the term «population» at a critical point in Kitcher's argument that Ghiselin-Hull theory, on Kitcher's interpretation in terms of his criterion, is incompatible with the biological species concept. This equivocation raises doubts about the general utility of historical connectedness as a criterion of historicality. The source of the trouble is that nothing follows from Kitcher's analysis about the relation between *species* and their members or parts without some further specification of the relation between *populations* and historical individuals. Kitcher has chased the problem to the level of populations, but has not sufficiently analyzed the concept of biological population for his argument to go through.

Because of this problem, I do not think 5a + 5b is a successful criterion of what makes a theory or science historical. But I have no general argument to show that a definition of historical connectedness cannot serve as the basis for a concept of historical entity. I have only claimed that without clarification of the concept «population» and the relation between population and species, Kitcher's use of the criterion fails as a criticism of Ghiselin-Hull theory. Extension of 5a + 5b to the concept of population may result in an adequate criterion. This would address the goal of proponents of claim 4 by identifying the source of historicality of a theory or science with properties of

the objects of study rather than with the methods or concepts, but by identifying a particular property other than temporal relation per se and thereby solving the problem with claim 4 raised above. But absent the extension, there is much cause for skepticism: the species problem is hard enough, and now the equally hard problem of population has been added to the task.

Where do these considerations leave us? The first four criteria are out and number 5 is open to doubt. Good-faith attempts to ground historicality in reference to multiple points of time, to prediction, and to directionality in the data have failed and the last, connectedness in time, has failed to establish temporal order in the phenomena definitively. I am led to try another avenue, one that ignores theory altogether and focuses on the historicality of a science.

Before characterizing historical science, I must introduce the concept of narrative sentence (Danto, 1985, ch. 8). To the extent that the analytical philosophy of history illuminates the general problem of what constitutes history, it will illuminate the concept of historical science. Danto's view of the role of narrative sentences in understanding history is significant for my argument: «My thesis is that narrative sentences are so peculiarly related to our concept of history that analysis of them must indicate what some of the main features of that concept are» (Danto 1985, 143).

My analysis of historical science is framed in terms of the concept of narrative sentences and a pragmatic criterion related to their presence in a science. As such, the definition of narrative sentence becomes part of the criterion of historicality of a science.

6a. A sentence is narrative if it refers to at least two time-separated events, but only describes, i.e. is only about, the earliest event to which it refers

Narrative sentences have a «teleological» character in that they refer to events in the future of a given event in order to describe and interpret the significance of the event. The sentence, «Malthus developed the basis for Darwinian evolutionary theory in *An Essay on the Principle of Population*», is narrative. It is about Malthus at the time of writing of this essay (published in 1978), but it refers in addition to something in the future of that event, Darwin's working out (in the 1830s) and publishing (in the 1850s) his theory of evolution by natural selection. The sentence describes Malthus in terms that lend significance to his writing due to events of which Malthus could not have known at the time. It selects his writing as significant among contemporaneous events in virtue of what happened later.

An important contrast between narrative and non-narrative sentences in biology stems from a grammatical difference between the relation «ancestor-of» and the relation «descendant-of». The sentence «*a* is an ancestor of *b*» refers to two objects, *a* and *b*. *b* is in the future of *a*, and *a* is the subject of the sentence, which is therefore narrative. In contrast, the sentence, «*b* is the descendant of *a*» refers to something in the past of its subject and is therefore non-narrative. The grammar of narrative sentences of the kinds found in systematic biology has not been well explored from a logical point of view, and I only mention it here to indicate problems and subtleties that await, especially for concepts like Kitcher's historical connectedness that refer to genealogical relations.

With Danto's concept of narrative sentence in mind, I can now define «historical science».

6b. A science is historical to the extent that is admits narrative sentences as contributing to understanding

Unlike claims 1 – 5, claim 6 (6a + 6b) differentiates explicitly between a historical science and a historical theory. This results from the concept of admission indicated in claim 6b. I have not specified what it means precisely for a sentence to be admitted into a science and I reject the idealized characterization of science as a «body» of knowledge and theory as a set of statements or sentences, but there is some sense in which the sentences circulating orally and in writing — among a community of scientists — are admitted into the science. I want also to distinguish between admission into a science and admission into theory (minimally because contradictory sentences may plausibly be admitted, consciously, into the former and not the latter). To be sure, there may be disagreement as to which sentences are admissible or have been admitted, and even lack of cooperation in the admission process, but admitted sentences are nevertheless «in play».

If one wants to characterize what it means for a *theory* to be historical, it is a virtue to make this parasitic on the concepts of historical science. Theory, at least in the grand sense implied by most philosophical work, is not necessarily the heart of a science and I do not see any reason to think the historicality of a science is any more dependent on the historicality of a theory than on the historicality of its data. So I characterize a theory as historical when it (however characterized) is put to use by scientists in a given science toward narrative purposes. Thus I think that evolutionary theory is historical because (some) evolutionary scientists use it for narrative purposes. I do not demand that, for example, population genetics theory be put to narrative use even if one accepts that theory as part of evolutionary theory because I do not demand that a science hang together very well or for very long.

To be too rigorous about such definitions is to do violence to the fragility of science as a process. If someone objects that then every theory is historical or not depending on usage and that we therefore cannot tell whether a theory is historical by inspecting its structure, I would reply that this is no objection unless the reasons to call for this independent means of assessment of theories are made clear. If someone prefers to claim that I have only defined the historical *use* of theories and not historical theories, I would not object: whether a *theory* turns out to be historical or not is not an important question.

I want also to make one further comment about the analysis itself concerning the role of narrative sentences in characterizing historicality. One reason I have chosen this route is to avoid some problems with thinking of narrative «linearly», that is, with interpreting narrative as stating single, unbranching causal sequences of events from A to B to C, etc. Robert O'Hara warns about producing linear evolutionary narratives. He points out that the subjects of

systematics are clades, and these «branched pieces of the evolutionary tree» lack some of the key properties of the sort of individuals that typically serve as «central subjects» in human narratives (O'Hara 1988, 152). Terminal taxa in a tree do not have continuity one with another, they are linked only by common ancestry. They also do not always have distinct endings in time, a property that O'Hara calls «closure». He observes that recognition of paraphyletic taxa is a means of imposing an artificial closure on an evolutionary group to «minimize the cladistic aspect of evolution and maximize the linear aspect (or rather create an imaginary linear aspect)» (ibid.).

Admission of narrative sentences as a criterion of historicality is intended not to prejudice the linearity or non-linearity of narrative. Since 6a only requires that a narrative sentence refer to at least two different times and that it be about only the earliest time to which it refers, nothing is implied about whether narratives must be linear or not. Whether a science, like systematics, is historical, is thus a distinct question from whether its narratives are or should be linear. O'Hara's «tree thinking» is compatible with a variety of conceptions of historicality and narrative structure.

This is important because it is open to question whether O'Hara's distinction between evolutionary history and evolutionary chronicle can be sustained. Danto characterizes chronicle as distinct from history as:

> ...just an account of what happened, and nothing more than that... [T]he very best kind of chronicle [which gives «all the details»] would still not quite be history in the proper sense... Proper history regards chronicles as preparatory exercises. Its own task is rather concerned with assigning some meaning to, or discerning some meaning in, the facts allegedly reported by chronicles. (1985, 116).

Following Danto, O'Hara claims that «*Systematics* is the discipline which *estimates* the *evolutionary chronicle*» (O'Hara 1988, 144; emphasis his). And evolutionary chronicle is the description of a series of events without accompanying «causal statements, explanations, or interpretations» (ibid.). I can accept, as does O'Hara, the distinction between history and chronicle as it is developed in the philosophy of history, but if this distinction is pressed into systematics along certain lines it will, I think, run into problems.

If O'Hara's view is that cladistic analysis is to phylogeny reconstruction as chronicle is to (narrative) history, then I disagree with his analysis on two scores. First, I think the practices of systematists tell against a distinction O'Hara tries to draw between human historians and systematists. He writes,

> In contrast to the historian, the systematist performing a cladistic analysis is trying to use all available evidence to estimate the position of as many evolutionary events as possible; he is not trying to construct a narrative account of a selected set of those events. (146-47).

Sober (1988), following arguments by Felsenstein, suggests that the question of available evidence is a complex one in systematics. The traditional view of advocates of parsimony methods for cladistic analysis has been that only shared derived characters (synapomorphies) provide evidence of cladistic relationships. But Sober and Felsenstein have both argued through consideration of maximum likelihood methods that there are evolutionary circumstances in which shared ancestral characters (symplesiomorphies) can also provide cladistic evidence. It is irrelevant here to try to decide which view of cladistic methodology is correct. My point is simply that what counts as available evidence is a negotiable matter in systematics. At the very least, choice of parsimony as a method does not lead to interpretation-free descriptions, so cladistic analysis produces something more theoretically charged than chronicle.

Second, while I agree that cladistic analysis aims at something prior to evolutionary narrative in the way that chronicle preceeds history, I think it is false to say that in performing cladistic analysis a systematist avoids the kind of selections among events that are essential to historical narrative. The «out-group method» for determining character polarity, for example, involves a selection from among a number of possibilities. But the selection process here is buried in the «craft work» of systematists that is not usually considered part of the cladistic analysis per se, e.g. in knowing or having hunches about what would make suitable out-groups, which is tantemount to a judgment of meaning or historical significance. Professor Urbani makes the even stronger claim that the simple choice of a statistical computer package performing maximum likelihood or parsimony methods is a declaration of faith in a given school of thought and that practicing systematists are well aware of such craft commitments (pers. comm.). My argument is with the artificial separation of craft work from high theory in the philosophical analysis of systematic practice. Moreover, Sober and Felsenstein have both vigorously argued that in order to do cladistic analysis at all, some model of character evolution must at least be tacitly assumed (Sober 1988, ch. 6). This imposes interpretive constraints and selection of data, based on events in the future of the branching sequences that cladistic analysis seeks to «estimate». For example, in assuming a neutral rate of molecular substitution, a model of character evolution refers to a process spanning the whole temporal duration of the clade being analyzed.

For these reasons, I think it will be difficult to pursue «a new philosophy of evolutionary biology», as O'Hara desires, «which reflects the discipline's historical nature», unless the practices of the discipline are articulated along with the central theoretical constructs that are usually identified with the core or essence of a discipline. I suspect that O'Hara agrees with this conclusion: he has begun the critique of such disciplinary practices (see his 1990, 1992), focusing on the character of evolutionary narratives (see also Landau 1984). In systematics there is a tendency to equate cladistic analysis with only the final step of running a computer program on a data set to produce trees. This is misleading about cladistic practice because most of the selection and a substantial amount of interpretation are implicit in the so-called «methodological» choices already made before a particular computer package is run. Neither do such methods thereby constitute a theory. It is therefore desirable to take as primary the historicality of a science so as to include all of the discursive practices besides those nominally connected with theory-structure, and to characterize the historicality of a scientific theory derivately.

Claim 6 entails nothing that compels evolutionary biologists to treat their science historically and nothing that precludes physicists from doing so. Historicality is a property that a science has in virtue of the pragmatic commitments that scientists make in

doing science. As such, it has no logical or physical necessity. Indeed, it doesn't even have social or cultural necessity: it is possible to practice a historical science ahistorically and an ahistorical science historically. Pragmatic commitments are negotiated parts of the social order of scientific practice, not fragments of epistemology or metaphysics.

To put this point in terms of the foregoing review of various attempted analyses of historicality, one need not refer to multiple points in time in order to describe a given moment of time. Failing to do so, however, leads to singularly uninteresting science, as the logical positivists showed with their protocol sentences as exemplary of ideal science («Otto senses a red patch in the upper left quadrant of his visual field at 4:05 pm, Thursday»). Their thought experiment in ideal science showed that not even the level of commitment to temporality required by claim 1 is logically or epistemologically necessary, but such commitments are pragmatically necessary if science is to be interesting.

One need not invoke the past in order to predict the future either. Claim 2 says nothing about how adequacy conditions for successful prediction are arranged in conjunction with conditions for *constructing* predictions, and even Hempel's symmetry thesis, which brings prediction under the same umbrella as explanation, is mute on this. So, there is a wide field for *deciding* to refer to the past in formulating predictions and their acceptance. Perhaps some general regularities will be discovered in the prediction-forming, -testing, and -judging habits of scientists, but I doubt it.

One need not invoke historical concepts in order to formulate scientific theories, either. In the discussion of the concept of adaptation above, the claim that this concept is historical was discussed. But even if accepted at face value, it is still open to biologists to operate without the concept. Using adaptation as an evolutionary concept requires commitment, one that neutral mutationists, for example, have tried at times to do without. It is certainly open to evolutionary biologists to change the scope of their science to exclude, as physicists have done, phenomena that seem to require concepts that do not meet their methodological «standard of taste».

One need not have intrinsic directionality «in the data» in order to commit to interpreting data historically. Temporal asymmetry is automatic in data, as I suggested, just in virtue of the fact that time itself has a direction and events and objects are located in time.

Finally, one need not have historically connected objects as subjects for a science to be historical. If Kitcher is right that the biological species concept allows species to be historically unconnected, then in so far as evolution was a historical science when the biological species concept was uncontested, it does not need historically connected objects. On the other hand, if it turns out that Kitcher is wrong and the biological species concept implies that species are historically connected, it is still plausible to think that evolutionists could proceed without their science being historical. They could, for example, embrace with enthusiasm what Dobzhansky reluctantly accepted as a working hypothesis in 1937: evolution is change in gene frequency. This commitment to the much maligned bean-bag genetical view of evolution, coupled with the view expressed in criticism of claim 2, that population genetics is just one more dynamical theory (and not thereby historical), would suffice to allow evolution to be practiced as an ahistorical science.

I doubt that my pragmatic criterion 6 will be warmly received. Certainly my criticisms of the other criteria do not constitute a rigorous argument in favor of my preferred criterion, though others reflecting on systematics have championed a pragmatic criterion of explanation, if not of historicality per se (see Ghiselin 1969, p. 29). Claim 6 seems to admit a rather literary quality of historical science that many have been at pains to avoid, for one or more of the reasons I discussed. But one virtue of the pragmatic criterion is that it highlights something the others have in common: they all try to find properties that make a theory or science *necessarily* historical. While I do think that the sciences can be demarcated, one from another and from other parts of society and culture, I do not think that seeking a necessary condition for a distinction among sciences as the first four criteria do is the right approach. The pragmatic criterion focuses attention squarely on two things: the social process of commitment and the nature of historical narratives. Many of the reasons for labelling a science (or theory) historical can be addressed by investigating a central feature of narratives: they assume a periodization of history which serves as a theoretical model in narrative construction. It is this aspect construction of theoretical models, that puts historical science on an equal footing with ahistorical science and defeats the hierarchical view of scientific authority. But natural historians have not articulated the view that their science is fully theoretical (Griesemer 1990). Analysis of the structure of theoretical historical models would go far toward answering the critics (Griesemer ms).

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Some thought on homology 150 years after Owen's definition

Abstract – During the last two centuries, several homology concepts, most often implicit but sometimes explicit and theoretically belaboured, have supported the most diverse research programmes, especially in comparative morphology, systematics and developmental biology. There seems to be no reason for restricting today the meaning and the uses of this term, e.g. only to historical, rather than biological, homology. These different traditional notions may be regarded as facets of a comprehensive notion of homology, with a major common background in the commonality of information lying behind the objects under comparison, but without any place for archetypes. The importance is stressed of always identifying the level(s) of description (hence, the type of homology) one is considering in a given study. The dangers of arbitrary atomistic descriptions is underlined. In a 'combinatorial' model of homology, a special, independent status is acknowledged to positional homology, as distinct from special homology: this point is supported by recent advances in molecular genetics.

How many homology concepts?

A homologue, wrote Owen (1843:374) in a well known passage, is «the same organ under every variety of form and function».

Owen was the first to systematically use the terms «homologue» (or «homology») and «analogue» (or «analogy») in a sense approximately equivalent to the sense (or, better, senses) in which we still use them. Things were different before, as one easily perceives, for instance, when studying Geoffroy Saint-Hilaire's «théorie des analogues» (e.g., Geoffroy Saint-Hilaire, 1807, 1818, 1830) where what is developed is a concept akin Owen's homology, rather than Owen's analogy.

There is no question as to the idealistic rationale of Owen's homology, but things are not simply set by stating, as seems to be implicit within some circles, that to implement Geoffroy's theory or Owen's definition all biology needed was simply the advent of evolutionary thinking, or the reformulation of historical homology concepts in terms of plesiomorphy and apomorphy (Hennig, 1950, 1966) or even identifying *tout court* historical homology with synapomorphy (Patterson, 1982).

But let me start a little before Owen, with a sentence typical of the best French morphology of the early nineteenth century.

According to Serres (1827:53), the great discovery of comparative anatomy had been «that those which are apparently the least similar one to the other are, however, fundamentally similar, and that, within the single individual as well as among the whole diversity of living beings, nature seems to have impressed two characters, the one perfectly compatible with the other, i.e. constancy within the type and diversity in the modifications» (my transl.).

This passage clearly sets the scope for a multidimensional research programme in comparative morphology (Minelli, 1995). A broader scope than the cross-specific comparative work we now understand, ever since Darwin and Haeckel, as phylogenetics. That means that the historical (genealogical) perspective, although prominent in the current agenda of comparative biology, does not exhaust the scope of this science. In other terms, equating homology with synapomorphy means reducing comparative biology to phylogenetics, and nothing else. We could also remark, a bit more fastidiously, that terms like «apomorphy», or «plesiomorphy», strictly refer to morphological or anatomical features, only by methapor being often extended to functional, behavioural, ecological or biogeographic ones. This point was aptly made by Tuomikoski (1967), when suggesting the use of the more comprehensive (but never used) terms «apotypy» and «plesiotypy».

If we look back at the history of homology research, we easily perceive that under this same term of homology several different traditions developed, with fluctuating success, ande several of them are still alive with us.

There seem to be several different ways of classifying these traditions, or the related homology concepts. For istance, a distinction between transformational and taxic homology has been widely employed, especially by cladists (e.g., Patterson, Rieppel, Cracraft, Eldredge, Panchen). This distinction somehow parallels but does not strictly identify itself with Wagner's (1989a) distinction between biological and historical homology concepts.

«Biological homology» rests on the identication of correspondance between biological properties, or processes, underlying the features under comparison, without any reference to genealogical relationships, or, more generally, to the temporal dimension at the geological time scale; the opposite holds for the historical homology concepts.

Wagner (1989a) regards these biological concepts of homology, with their reference to biological mechanisms rather than to genealogical relationships, as more inclusive than the historical ones. I would rather regard them as complementary and worthy of inclusion in a broader construed notion of homology.

Much of the trouble with homology, especially in the recent literature, has to do with quite opposite attitudes at this starting point: whether, I mean,

the only possible meanings of homology have to be searched for in a historical perspective, or, on the contrary, there is still also a scope, even in a post-Darwinian era, for non-historical, but nonetheless meaningful, concepts of homology.

I do not intend to approach here this question in a philological vein, i.e. by tracing, work after work, the origin and the fate of individual terms, like homology, homonomy, homodynamy etc., in order to apply some kind of priority rule, as does, for instance, the International Code of Zoological Nomenclature for the scientific names of animal species. I am well aware that my concept of homology, in so far as it receives the legacy of different research traditions, is perhaps too diffuse to be adequately covered by a single, universal term, but I feel that, at present, concepts and corresponding terms may profit from a global discussion within a broader context, before risking a recrystallization under old or new wordings. A similar attitude towards homology has been defended by Ghiselin (1976) and Haszprunar (1992), with whom I am largely in agreement.

Nor shall I reiterate here the arguments developed elsewhere (Minelli & Peruffo, 1991; Minelli, 1992; also Ghiselin, 1976; Haszprunar, 1992, and others) as to the opportunity of keeping within one comprehensive concept of homology both inter- and intraindividual relationships, as those traditionally labelled as special homology and serial homology. Rather, I shall examine in some detail a few premises, and a few consequences, of such a catholic approach.

Due to the multidimensionality of comparative biology and to the lack of congruence between the different aspects of 'sameness' (Wagner, 1994), a prerequisite for any non trivial use of homology will always be a clear identification of the subset of possible homology components (e.g., positional homology; or historical homology) we are dealing with in a given study.

Inadvertently skipping from one kind of comparison to another leads all too easily to dangerous situations. A serious difficulty is still very well entrenched in the literature dealing with the old issue of ontogeny vs. phylogeny.

From a phylogenetic point of view, one possible way to look at evolution is to regard it as a history of changes of ontogenetic programmes. Accordingly, the topology of these changes across geological time is nothing but the topology of the phylogenetic tree. But many evolutionary changes involve heterochronies, or other modifications of the developmental schedules, such as to limit the applicability of Nelson's (1978) reformulation of the biogenetic law. According to Nelson (1978:327), «given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general advanced. «But this is right the starting point for Patterson's (1983) identification of ontogeny and phylogeny. I fear that both Nelson (1978) and Patterson (1983) have fallen victims of Zeno's paradox. Achilles will never reach their turtles, because Zeno, Nelson and Patterson have limited a priori the context (a temporal framework in Zeno, a relational one for pattern cladists) where their game has to be played. The world, however, is wider. Nelson's and Patterson's too selective principles work well, perhaps, but only within the limits set by a strict pattern cladistic approach, where homology cannot be other than synapomorphy, as verified through the three classic tests of Patterson (1982).

The dangers inherent in this pattern cladistic approach are seldom so evident as in the following statement one can read in Alec Panchen's (1992) book on «Classification, Evolution, and the Nature of Biology». We read there, on p. 5, that «If the pattern of classification is logically prior to phylogeny [a firm point, in pattern cladists' view], the characters on which it is based should have logical priority over the pattern. There should therefore be a Natural Hierarchy of characters, whose similarity in all the members of a taxon is recognized as homology».

In spite of the use of terms like phylogeny, or evolution, it is here, rather than in a non-phylogenetic approach to homology, that I perceive an old-fashioned attitude towards comparative biology. I think that we do not necessarily (better, not always) need to find out a priority criterion for characters; but, whenever we need one, why, if not in an essentialistic framework, are we to look for a logical, rather than an historical, criterion?

I do not go further with this argument. Rather, it is perhaps worthy of careful investigation what happened to Geoffroy's *analogie*, or Owen's homology, after the publication of the «Origin». Here, however, I will only offer some suggestions.

On the one hand, the well-known idealistic exaggerations of the last century do not seem to be completely dead. Most people will probably regard as long extinct that early ninenteenth century tradition of *Urpflanzen* which, belabouring Goethe's morphological speculations, produced those unbelievable summaries of possible forms we could only define as hopeless monsters; see, e.g., Turpin's (1837) picture of an hypothetical *Urpflanze*, recently reproduced by Mägdefrau (1992).

In the recent literature, there is still a place for 'ground-plans' (for a reasonable example, see Enghoff's (1990) chilognathan millipede) but these rather run the apposite risk, to be too poor in structure as to correspond to possible living animals: in fact, they are mainly built on the basis of a few better founded synapomorphies of a higher taxon, and nothing else.

But let me read from the recent (and otherwise attractive) book of Nijhout on butterfly wing patterns: «The nymphalid ground plan represents the maximal pattern that is found in the family Nymphalidae. However, no species is known that has all the elements of the nymphalid ground plan in its wing pattern» (Nijhout, 1991:27).

On the other hand, it is fair to say that such slippings are, overall, rare. Problems with the tradition of rational morphology are mostly of the opposite nature.

In his «Strategy of Life» (1982), Timothy Lenoir has argued that the success of the research agenda developed around Darwinian evolutionary theory caused obfuscation of the German and French comparative morphology developed between the last decades of the eighteenth and the first decades of the nineteenth century. In this vein, one could specifically argue that one effect of this change of mind was the more or less conscious restriction of homology to an historical framework.

It is also fair to say that, until recently, hardly a mechanism was available as a possible explanation for the structural patterns around which developed the speculations of a Vicq d'Azyr, or a Geoffroy Saint-Hilaire. Things are different today, however, and that seems to me much of a good reason for resurrecting (or, better, translating into more modern terms, as we will see later) many concepts of the old rational morphology.

Wagner (1989a, b; also with reference to de Beer (1971) and to Roth (1988)) has recently argued that «It seems implausible that continuity of gene lineages alone could account for the homology of morphological features». More recently, Kauffman (1993) contends that there is a scope for a non-historical approach to biological organization. This approach more or less merges with the structuralist tradition. Structuralism and Darwinism have been often regarded as unreducible opposites, and a lot of structuralists' excesses well justify this claim, but things do not need to be so. In a very important paper of 1987, Wake & Larson have convincingly argued in favour of a synthesis of structuralism and Darwinism and I cannot but subscribe to their program. In this perspective, I believe that a suitable, and adequately broad concept of homology will play a non-trivial role.

Units of description

«It would be impossible to understand about what we are talking, says Riedl (1980:157; my transl.), whenever our terms were not rooted in homology».

In this vein, it is all but difficult to understand why, ever since Cuvier, people seem to feel so sure, when partitioning the Animal Kingdom into a suitable number of *embranchements*, or phyla. Less often consciously than not, zoologists feel free from any obligation to look for homologies, when taking together (I do not say «comparing») animals they have placed in two different phyla. Cross-phylum homologies are, more or less by definition, doubtful, uncertain, speculative; something that most good zoologists feel, or felt, not obliged to follow up. At least, it was so before the advent of comparative molecular biology. An all too easy solution, anyway. Let us look, for instance, at the prompt dissolution of the traditional phylum Arthropoda in the hands of Sidnie Manton, as soon as she found herself in trouble with things such as the homology between the gnathobasic mandible of chelicerates with the tip-working mandible of insects and allies (her Uniramia).

Well, homology serves as a universal foundation of our scientific discourse. But, to begin with, homologies between what? In morphology, as in other sciences (e.g. in descriptive geology; Laudan, 1992), oe major problem is the proper identification of suitable units of description and comparison.

As Eldredge & Cracraft (1980) posed it, every comparison cannot but begin within 'comparable' units. «But what does 'comparable' mean? — asked Nelson & Platnick (1981:151-2) — Are not all things 'comparable'? Potentially yes, but actually biologists do not compare arms with eyeballs or noses (although there is not rule that biologists may not do so). They compare, for example, arms of a human, or wings of a bat, with the fore legs of a frog or the pectoral fins of fishes. To a biologist, these organs display interesting similarities and differences, interesting perhaps only because a biologist can generalize about. And by stating that they are homologous, one means at least that general statements can be made about them».

In other terms, «The significant point is that for any discussion of homology, homologues must first be recognized based on similarity. The primacy of similarity over phylogeny puts an onus on morphologists to be able to apply similarity to identified morphological elements» (Young, 1993:235).

Can we subscribe to Young's posit? Before answering this question, it is perhaps apt to underline, how loose is the current use of the term «morphology», which is often understood as a plain synonym of «anatomy», sometimes retained in his original and legitimate meaning of study of (abstract) form, and all too often dangerously employed to mean both of those things. Now, moving back to the foundations of homology, it seems to me that similarity, as such, can only be the background of that 'operational notion of homology' (i.e., something that actually has nothing to do with homology proper) such as developed within the domain of phenetic, numerical taxonomy (Sokal and Sneath, 1963; Sneath and Sokal, 1973; cf. also Patterson's (1982) historical review of homology concepts). Within an evolutionary context, things go on otherwise.

A good morphologist, to begin with, is well aware that there are many different possible levels of description. Therefore, the first aspect to care for is to avoid mixing, in a given comparison, concepts and terms pertaining to different facets of morphology or anatomy. In a well-argued analysis of homology problems in the study of animal body cavities, for instance, Remane (1963) distinguished between (a) descriptive-histological terms such as gymnocoel and epitheliocoel, (b) ontogenetic terms such as schizocoel, enterocoel, neocoel, (c) morphological terms s.str. such as amniotic cavity, and (d) functional anatomical terms like haemocoel.

Nevertheless, this is just the starting point. More often than not, it is quite difficult to perceive how traditionally biased are our current circumscriptions of only apparently trivial terms, like flower and inflorescence in plants or head, thorax and abdomen in animals.

First, a botanical example. In a conventional hermaphrodite flower, there is a standard sequence of whorls: begininng with the outmost sepals, we usually find petals, followed by stamens and finally carpels. In lieu of sepals+petals, there is sometimes a single kind of external, nonreproductive elements (tepals); in addition, any one of these whorls may be missing, but — this is the main point — their order is never reversed. At least, botanists do not allow them to be. However, to the scorn of typological botanists, there actually are a few kinds of flowers where the sequence of whorls is: outer tepals, outer ring of stames, inner tepals, inner whorl of stamens. When confronted with such an arrangement, «the classical minded phytomorphologist refuses to accept the configuration [..] as representing a flower, but declares it to be an 'inflorescence' (more precisely: a pseudanthial inflorescence)» (Meeuse, 1986:10). In a sense, positional constancy has become a kind of de-

fining property for the parts of a flower. But, is this attitude truly justified? I do not think so. The newest discoveries in developmental genetics of plants have shown that not just the shape and the colour, but also the relative position of the floral elements is under relatively simple genetic control. The fact that the usual order is seldom reversed does not imply that it cannot sometimes be upset, as in some laboratory mutants. Surely no developmental genetist would surely argue that an *Antirrhinum* or an *Arabidopsis* with its petals and stamens in unconventional sequence is something different from an (admittedly odd) flower. Interestingly enough, Martínez and Ramos (1989) have recently discovered a plant species (*Lacandonia schismatica*) with literally inverted floral whorls, the stamens being encircled by the carpels!

Let me now skip to a zoological example. I do not intend to discuss here whether there is any sense in giving the same name (head) to the foremost section of the body of the swordfish (a vertebrate), the silverfish (an insect) and the cuttlefish (a mollusc), although this question, to a belated vengeance of Geoffroy Saint-Hilaire ad his disciples Meyranx and Laurencet, could be perhaps less crazy than it seems to be (see later).

Here, however, I wish to point to the difficulties in determining what a thorax is in aculeate hymenopterans, where, as it is customary to say, the first abdominal segment is incorporated within the thoracic tagma. Why not to say that the boundary thorax/abdomen runs here one segment behind its usual position in insects?

Again, is it more meaningful to say that the first thoracic segment is fused to the head in woodlice and allies (Isopoda), or to acknowledge that the position of the head/thorax boundary is not universally the same within crustaceans?

According to Boxshall & Huys (1992:332), «Tagmata separeted by boundaries that lie in different location cannot be compared. For example, maxillopodans such as copepods, thecostracans and tantulocaridans cannot be grouped together with the Malacostraca on the basis of the division of the postcephalic trunk into two tagmata (thorax and abdomen) because the tagmata of maxillopodans and malacostracans have a different somite composition and are not homologous. «In other terms, according to Boxshall & Huys tagmata are homologous in so far as the boundary between them lies in an homologous position. But, how is this positional homology to be determined? Is the usual count of segments, with a more or less hypothetical acron as number zero, a universally reliable reference? I do not think so. To back my argument, I simply refer the reader to the example in Figure 1, which I have discussed in more detail in a recent paper (Minelli, 1992).

A good morphologist is able to avoid these semantic pitfalls, but the circumscription of characters to consider for homology statements still requires addressing and possibly solving additional questions. I shall shortly touch on three points.

A first question relates to the contrast between atomistic vs. holistic approach.

Wagner (1989a:58) has rightly stressed that «lack of developmental individuality of parts may render the identification of structures meaningless», but one cannot be sure, at the outset, that a thorough knowledge of morphogenesis will grant recognition
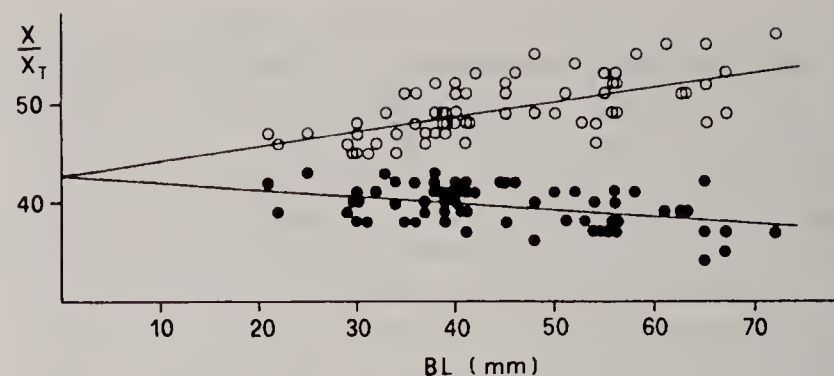
Fig. 1 - How to compare position along the body of a segmented animal, if the number of segments is not constant within the species? A relative position (such as the 35% of the total number of body segments, as determined in antero-posterior direction) may be more meaningfully comparable than an absolute position (such as the 35th segment). At least, so is the case illustrated in the figure.

In the very slender, worm-like centipede *Stigmatogaster gracilis* (Chilopoda: Geophilomorpha), the number of body segments is quite variable, even within a single population. However, segment number does not increase with age: through the several moults they undergo during their post-embryonic life, these animals retain the number of segments they possessed at birth. In a few segments, which form an uninterrupted series a bit before mid-length, the ventral plate (sternum) is 'marked' by the presence of a pair of lateral grooves. The number of sterna with grooves increases with age. In addition, in the animals with a smaller total number of segments the grooves occur in more anterior segments than in animals with more segments. However, the relative positions always remain the same, as demonstrated by the figure, which shows the linear regressions separately calculated for the relative segmental position of the first and last segment with grooves (black dots and open circles respectively) vs. body length (BL), as observed in 66 Italian specimens of this species. Relative segmental positions (X1/XT) are calculated by dividing by the total number of leg-bearing segments (XT) the actual segmental position X where the groove series respectively begins or ends. For both regressions, $p<0.001$ (after Minelli, 1992; reproduced here with the permission of the publisher, Universitätsverlag Wagner, Innsbruck).

of individual (atomic) units of comparison. This is the message conveyed by Goodwin and Trainor's (1983) theoretical analysis of digit differentiation in tetrapod limbs. They contend that homologizing limb elements involves an artificial atomism, whereas, in their opinion, individual skeletal elements do not have an identity of their own. Rather, Goodwin and Trainor's holistic-structuralistic approach recognizes the whole limb as an integrated developmental field. In their view, when confronted with a 4- or 3-digit limb, we cannot say that one or two digits are missing, e.g. the first or the fifth. What they regard as the only meaningful comparison is one involving the whole of the digit-forming material present in the two instances: a digit-forming material that, in the case of the digit-reduced appendages, only reaches for 3 or 4 digits, rather than for the 5 of ... how to say?, the 5 traditionally supposed to have been present in the archetypal tetrapods (but see the recent evidence for a larger number of digits in early forms like *Ichthyostega*; Coates and Clack, 1990).

I am sincerely ready to take Goodwin and Trainor (1983) seriously, is spite of the difficulties raised by Shubin & Alberch (1986:375), who claim that «if Goodwin & Trainor (1983) took their approach to its logical conclusion, they could not discuss limb development and evolution in the first place, since this requires them to use concept of homology at another level of the taxonomic hierarchy – to homologize a structure called a limb in the first place. They implicitly accept a certain degree of compartmentalization

by assuming that the limb is an independent embryonic field [..] The degree of developmental compartmentalization corresponds to the level at which homologies can be resolved».

The challenge of the holistic approach has been recently extended into a field that most developmental biologists regard as a triumph of the genetic dissection of a complex pattern, that of the origin of body segmentation in *Drosophila.* In the study of this developmental process, a whole gallery of 'segmental monsters' opened the way to a wonderful genetic analysis, beginning with Nüsslein-Volhard & Wieschaus's (1980) already classic paper. This analysis progressively revealed the individual role of a lot of genes, in establishing the main features of body architecture and of segmentation in particular. Of many of these genes we now know both the sequence, the spatial and temporal patterns of expression and the interactive effects with the products of other genes. Well, right against this compact body of experimental data, which all point in favour of the individual roles of individual genes in controlling specified aspects of body structure, Goodwin's group (Ho et al., 1987) have shown that *Drosophila* embryos, exposed to ether between 1 and 4 h after deposition, often develop segmentation defects resembling known mutant phenotypes. Their conclusion is, that «at least part of the segmentation process may consist of physicochemical reactions coördinated over the whole body» (p. 511). Quite independently from the final judgement on the mechanisms actually involved in digit formation in vertebrates, or in body segmentation in insects, I once more want to stress the danger of rushing towards atomistic descriptions and, hence, comparisons.

This point, however, still leaves us with the question: where to begin? Perhaps — this is my second point — with archetypes?

Young (1993:225) has recently argued «that neither the concept of «structure» nor that of «homology» can be incorporated within a morphological science that lacks an archetypal foundation. By an archetypal concept I mean the recognition of stable underlying patterns within morphological systems».

From an ontological point of view, this «archetype» seems to be immanent rather than transcendant, thus quite different from Owen's one. Nevertheless, it is still an essentialistic, rather than an empirical, construction.

Worries in front of this persistent ghost of archetypes seem to be largely responsible for the widespread shift of attention, in the literature, from transformational, or biological, to taxic, or historical, homology. For instance, Patterson (1982) only accepts the taxic notion of homology as synapomorphy, stating that transformational homology is always validated by reference to archetypes. However, as also asserted by Panchen (1992:71), things are not necessarly so, if our transformational comparisons rest, apart from Geoffroy's principle of connections, on the identification of similar developmental pathways in ontogeny.

Summing up, I do not believe that the ghost of archetypes should be raised against transformational, or biological, homology, any more than against taxic, or historical, homology. As we have already seen, both of them are able to generate groundplans, or Ur-somethings. On the contrary, both of them may (and should!) content themselves with a minimum requirement of starting hypotheses, when adopting a given set of terms for describing, at the outset, the objects to be later compared.

Moving soon to the third, and last, point of this section, a major trouble for students of homology has long been the fact, that features regarded as homologous are sometimes built, in different organisms, under the control of different genes. A more recent version of this problem is Roth's (1988:7) 'genetic piracy', when «genes, previously unassociated with the development of a particular structure, can be deputized in evolution, that is, brought in to control a previously unrelated developmental process, so that entirely different suites of genes may be responsible for the appearance of the structure in different contexts».

I believe that in order to assess the actual relevance, or even the meaning, of Roth's genetic piracy, we would need a better knowledge of what we could call the redundancy of genetic control over developmental pathways. Leaving aside the experimental aspects of the question, I feel, from a theoretical point of view, that to ignore this redundancy is one aspect of well-entrenched typologism and reductionism.

On the contrary, recognizing that the features we are homologizing are subjected to a redundant control, or that their history has seen episodes of genetic piracy, is not a problem, whenever we develop a combinatorial view of homology, as outlined below.

An informational and combinatorial view of homology relationship

Developmental biology has often demonstrated that the same body part can often be built out of materials with different origins. What is required, to get those organs, seems rather to be the spread of some specific information through previously inert materials. Some example follow, from a potentially enormous literature (cf. Wagner 1989a), just to give an idea of the different levels through which this phenomenon spans.

Norris (1993) has shown that there is considerable flexibility in the makeup of the tympanic bulla, with variable incorporation of the squamosal into the tympanic floor, within the same population of a marsupial, the grey cuscus (*Phalanger orientalis*).

At the other extreme of the possible taxonomic range, within Metazoa, our current awareness of comparative embryology suggests that the contribution of germ layers to various body parts can vary to such an extent as to undermine the very concept of germs layers.

Even an apparently major difference, such as that between cells vs. syncytia, seems to be of minor importance, e.g. in some steps of insect body segmentation, as shown by a comparison of *Drosophila*, with its syncytial blastoderm, with the lesser flour beetle *Tribolium*, with cellularized blastoderm (Sommer and Tautz, 1993).

Writing on homology right 50 years ago, Boyden (1943:233-4) expressed the view that «Homology is a genetic phenomenon». This may sound like a simplistic, reductive view of the problem; nevertheless, it can serve as a suitable starting point for the following argument.

I identify three major attributes of a biological concept of homology. Two of them are the informational background and the relativity of homology (cf. Minelli & Peruffo, 1991, and references therein), from which we can easily derive the third point, i.e. the compositional aspect of homology. This approach (Minelli, 1992, 1993; Haszprunar 1992) seems to me a way of integrating more strictly the different kinds of homology as identified by the old comparative anatomy and more recently redefined by Ghiselin (1976).

The individual features of the phenotype are the outcome of a series of developmental choices (more or less directly mapping onto the genome), many if not most of which can be identified, in principle, as independent units of developmental control, either as morphogenetic or as morphostatic constraints (Wagner, 1993). In principle, again, we can separate the processes leading to these developmental choices or control, as individual components of the overall informational background underlying a given feature and, by consequence, its homology with corresponding features of the same organism (serial homology) or of different organisms (special homology).

A notion of relativity also solves the problem of the lack of unbound transitivity in homology relationships, to which Paulus (1989:472) recently called attention.

Adopting this conceptual framework may also help addressing the interpretation of the so-called 'intermediate' structures, which seem to take part of two or more different elements and are often, too often, described in terms of 'fusion of structures' whereas, especially in ontogenetic terms, they would much better be described as 'nondisjunct'. Once more, a botanical example: «If a shoot apex does not differentiate lateral primordia, but remains a smooth protuberance until it starts growing (i.e., increasing its volume by cell divisions and cell stretching), something like the corm of a lemnaceous plantlet develops. There is no 'fusion', but 'lack of separation'; the resulting cormoid structure is unclassifiable as a 'stem' or 'a leaf' and to call it 'intermediate' is highly questionable; it is rather a chimeric merger» (Meeuse, 1986:14-15). I would like to describe in the same terms a lot of structures occurring in the animal kingdom, as the so-called diplosegments of millipedes, which are clearly 'double segments' ventrally, but 'unitary' dorsally.

Positional homology in developmental mechanics and in comparative anatomy

The search for a suitable reference system within which to identify homology relationships has often moved away from the tangible realm of histology and anatomy proper, to develop in more abstract, geometrical terms, as in D'Arcy Thompson's (1917, 1942) coordinates and transformations, or, more recently, within the new morphometrics of Fred Bookstein and associates (e.g., Bookstein et al., 1985; cf. also Rohlf & Marcus, 1993 but see Bookstein (1994) for a recent rethinking on these matters, ending up with a strong denial of the possibility of reconcile morphometry with a search for homologies).

However, one could more legitimately search for, so to say, intrinsic coordinate systems, as already did Geoffroy Saint-Hilaire, who suggested that the network of blood vessels could provide a kind of scaffolding against which to identify topographical relationships. More recently, rather than the vascular supply to the different body parts, other connecting elements, such as muscles and especially nerves, progressively gained in favour among comparative anatomists, as suggestive of identifiable positions and, hence, of homologies (cf. Remane (1963) for a modern assessment of these matters). On the whole, the relationships between nerves and innervated organs are generally held as the most reliable. One wonders whether the reliability of inferences of homology from nerve connections may be justified by the role of nerves as morphogenetic tracers. However, as noted by Bock (1989:338), such «Positional tests [of homology] are not as simple as they appear. A common one is to test the homology of skeletal muscles by their innervation, using the assumption that the same nerve innervates homologous muscles even when the muscles change shape and bony attachments drastically. In such tests, it is necessary to first establish the homology of the nerves independently, which is not an easy task, especially when one is dealing with secondary and tertiary branching of a nerve».

At any rate, things seem to be different in different systems; see, for instance, the results of Broadie & Bate's newest investigations (1993:350). In the embryo of *Drosophila*, individual motor neurons form stereotyped synapses on individual, identified muscles. Broadie and Bate «used a mutant (*prospero*) that removes or delays innervation to assay the role of the presynaptic motor neurons in the development of the receptive field of the postsynaptic muscle. *Prospero* (pros) is not expressed in the muscles or their precursors. [They] find that the muscle defines the correct synaptic zone in the absence of the motor neuron by restricting putative guidance molecules to this specialized membrane region. Furthermore, the muscle expresses functional transmitter receptors at the correct developmental time without innervation. On the other hand, the muscle does not localize receptors to the synapse without instruction from the motor neuron, nor does a second, much larger, synthesis of receptors occur in muscles deprived of innervation». These results suggest that, in this system at least, the role of muscles is not simply a passive one, where all connections are specified in advance by nerves.

However, even if a mechanistic, i.e. molecular, interpretation of the primacy of nerves in establishing a morphological reference system within the animal may still sound doubtful, there seems to be much scope for a molecular interpretation of the *Lois des connexions*, especially at the level of gross morphological organization.

Let me introduce this point by focussing on an elementary, but generally overlooked feature of comparative anatomy. Within the body architecture of all animals, there are some 'hot spots' where many, or most, of the key features of the body differentiate and evolve. In most groups, the most conspicuous of these hot spots are the two ends of the body, but there are also other, less conspicuous 'hot spots', a few of which seem to be worthy of attention.

Take, for instance, a male dragonfly. At variance with the generality of insects, it has not developed a copulatory structure in strict anatomical connection with its genital opening, but one several segments in front of it. This morphological behaviour is quite strange, although not unique within Metazoa, but I am not recalling it here to discuss its origin, or to trace any special homology of this secondary penis to structures in other insects, but simply to point to an unexpected topographical correspondence. In fact, male gonopods in most millipede families are the modified appendages of what seems to be exactly the 'same' segment as that with genital opening in dragonflies, whereas the secondary penis of dragonflies occur at the same segment where male millipedes have their genital opening! These two segments also behave as a kind of 'hot spot' (Minelli & Schram, 1994) where different arthropods are able to specify different highly specialized structures. Why do all these structures develop there, in spite of their very different nature? Probably because the 'hot spots' are evolutionarily homologous and have not changed their relative position, at least since the lineage leading to dragonflies split off from that leading to millipedes. I see here a kind of positional homology, despite a lack of special homology.

Recently, Slack et al. (1993) have tried to characterize what they call the 'zootype', a kind of molecular archetype of metazoans. This zootype would be under the specific control of the so-called Hox genes. Not that these genes actually specify any given structure, such as mouth, brain, heart, kidney, or anus, but they seem to lay down the general scaffolding of the body, by giving — in molecular terms — positional value to the different points along the main body axis.

I believe (cf. Minelli & Schram, 1993) that these facts and models (the zootype; the segments with secondary penis in dragonflies and gonopods in millipedes) are better discussed by reference to what may be regarded, in a sense, quite the opposite. I am thinking of the homoeotic mutants, where, in spite of the different positional specification, there is still a point-to-point structural correspondence (iterative homology) between the normal feature, e.g. a leg, and its ectopic counterpart. On the other hand, the position of the ectopic leg of an Antennapedia mutant is the same as that of a normal antenna in a wild type fly. But, when I say 'in the same position', I imply a kind of 'positional homology', to be evaluated independently from the «special homology» between the appendages. But current molecular genetics of development allows us to give a material meaning to this positional homology, not less tangibly so as it gives a material meaning to the special homology of structures whose differentiation we envisage as dependent on similar genetic control. — Let me add, incidentally, that to speak of 'ectopic legs', as is customary, literally implies wrong interpretations of facts: the expression implies that a leg has somehow changed its position, whereas it is another appendage that has differentiated with properties that usually are expressed in other positions.

Summing up, in this application of the concept of compositional homology mentioned before, there seems to be scope for three interestingly different kinds of comparisons: (a) those with conservation of positional homology, but not of special homology, (b) those with conservation of special homology, but not of positional homology; (c) those with conservation of both kinds of homology, positional and special.

The positional specification of the main body axis seems to be only one of the systems where these Hox genes are involved. In vertebrates, they also seem to function during embryogenesis of other structures, such as the limbs, the skeleton and the nervous system, where regional variation of the components must be established along axial coordinates (Krumlauf, 1993). In other instances, as in the development of insect appendages, there appears to be an element of polar coordinate reference systems (Bryant, 1993). This polar system is coupled with a «segmentation» process similar to that of the main body of arthropods wherein protein markers of annulin mark the limbs boundaries (Bastiani et al., 1992).

Positive knowledge of these genes, of their expression patterns during early embryogenesis and of the relationships between corresponding Hox genes in different metazoans are rapidly increasing. But we do not need to wait for much experimental detail, before we dare to suggest — right as a kind of research programme for comparative molecular geneticists — a reinterpretation of many facts of traditional zoological wisdom.

Why is the anatomy of flatworms generally so unstable, compared to that of insects or vertebrates? (Russell, 1930). Is perhaps this fact a consequence of the lack of a hot spot at the rear end of the body?

Once established, body landmarks (hot spots) topographically constrain subsequent morphogenetic events (Minelli and Schram, 1994).

For instance, in digenean trematodes a mid-body spot sets the site for the genital opening only, whereas in planarians both mouth and genital opening appear there.

Again, in male nematodes a posterior, subterminal spot marks the cloacal opening, whereas in females only an anus develops, the genital pore being borne on an additional mid-body spot. And so on.

Adopting a compositional view of homology and, especially, extracting positional homology as a factor of its own, poses many new, interesting problems. For instance, whether there is a minimum size for discrete pattern elements, as one could see, for example, in the subcellular kineties, acting as templetes for ciliary structures in ciliates (Frankel, 1989). One interesting feature is, that some animals are perhaps too small to get more than anterior/posterior polarity, e.g., dicyemid mesozoans. Others are too small to develop or retain segmentation, e.g. eriophyid mites (ca. 50 μm). This fact suggests a possibly interesting field of investigation, that of the grain of biological forms. Of course, the same animal or plant will turn out to be fine-grained or coarse-grained according to the criteria of description. There is no 'absolute' grain. Nevertheless, I think that comparative morphology and evolutionary biology both have much to learn from studies such as those of Shimizu et al. (1993) on *Hydra*, or Weber (1992) on *Drosophila*. Shimizu et al. have tried to determine the minimum tissue size required for regeneration in *Hydra*; this size turned out to be some 270-300 epithelial cells, the minimum number of cells that proved to be required for going through the critical stage of hollow sphere, before starting re-differentiation towards the polyp form.

On selection, rather than regeneration, was the focus of Weber's study. He tried to see, in his words (p. 345), «whether the necessary genetic potential exists for dense, finegrained, autonomous and localized adaptive change all over the insect wing; or whether the potential for localized remodeling is only coarse-grained and scattered here and there». In selected cases, a very small wing region, of less than 100 cells across, did respond to selection almost independently from the behaviour of the neighbouring cells. Weber concluded that «the control of developmental detail must involve many genes, and the diversity of possible outcomes in development and adaptation must be large».

Concluding remarks

To conclude this walk through the world, or worlds, of homology: far from being an empty, or useless or deceptive, old-fashioned concept, as many students have contended in a not too distant past, homology still occupies a central place in comparative biology. Far from annihilating it, advances in genetics and developmental biology have contributed many valuable findings and ideas, on the basis of which our appreciation of homology has progressively improved. Finally, molecular biology provided the stuff for clearing the field from that lasting ghost of subjectivity, the criteria for positional homology.

But this does not simply mean that homology has no necessary connection with phylogeny, i.e. with history, with time. Rather, it turns out to be the central, though multi-faceted concept of a comparative biology whose agenda we should perhaps articulate in revised, explicit terms, 150 years after Owen's definition of homology.

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Trees of history in systematics and philology

Abstract — «The Natural System» is the name given to the underlying arrangement present in the diversity of life. Unlike a classification, which is made up of classes and members, a system or arrangement is an integrated whole made up of connected parts. In the pre-evolutionary period a variety of forms were proposed for the Natural System, including maps, circles, stars, and abstract multidimensional objects. The trees sketched by Darwin in the 1830s should probably be considered the first genuine evolutionary diagrams of the Natural System — the first genuine evolutionary trees. Darwin refined his image of the Natural System in the well-known evolutionary tree published in the *Origin of Species,* where he also carefully distinguished between arrangements and classifications. Following the publication of the *Origin,* there was a great burst of evolutionary tree building, but interest in trees declined substantially after 1900, only to be revived in recent years with the development of cladistic analysis.

While evolutionary trees are modern diagrams of the Natural System, they are at the same time instances of another broad class of diagrams that may be called «trees of history»: branching diagrams of genealogical descent and change. During the same years that Darwin was sketching his first evolutionary trees, the earliest examples of two other trees of history also appeared: the first trees of language evolution and of manuscript genealogy. Though these were apparently independent of evolutionary trees in their origin, the similarities among all these trees of history, and among the historical processes that underlie them, were soon recognized. Darwin compared biological evolution and language evolution several times in the *Origin of Species,* and both Ernst Haeckel and the linguist August Schleicher made similar comparisons. Both linguists and stemmaticists (students of manuscript descent) understood the principle of apomorphy — the principle that only shared innovations provide evidence of common ancestry — more clearly than did systematists, and if there had been more cross-fertilization among these fields the cladistic revolution in systematics might well have taken place in the nineteenth century.

Although historical linguists and stemmaticists have in some respects had sounder theory than have systematists, at least until recently, they have also had the practical problem of very large amounts of data, a problem not often faced by systematists until the advent of molecular sequencing. The opportunity now exists for systematists to contribute to the theory and practice of linguistics and stemmatics, their sister disciplines in historical reconstruction, through application of our commonly used computer programs for tree estimation. Preliminary results from the application of numerical cladistic analysis to a large stemmatic data set have been very encouraging, and have already generated much discussion in the stemmatics community.

Introduction

In a series of influential papers beginning in the 1960s, Michael Ghiselin challenged a view common among philosophers of science that species, the basic unit of systematics, are best thought of ontologically as natural classes (Ghiselin, 1966, 1974, 1984, 1987). Rather than seeing species as classes of organisms, Ghiselin argued that they should in fact be regarded as complex, historical individuals: singular things which have particular spatial and temporal distributions, and which have individual organisms as their *parts* rather than as their members. Although this view of the ontological status of species was initially rejected by many philosophers, it has since come to be widely accepted (Hull, 1975, 1978; O'Hara, 1988b).

Although Ghiselin was primarily concerned with the ontological status of species in these papers, it was implicit in his position that higher taxa must also be individuals in a certain sense (Ghiselin 1984: 85), individuals made up of species which are their parts, just as any whole human body is made up of individual organs. In this paper I have two aims. The first aim, following Griffiths (1974), de Queiroz (1988), and my own earlier work (1993), is to develop the notion that higher taxa are ontological individuals or *systems,* as Ghiselin had implied, and to demonstrate that reflective systematists have long regarded them as such. My second aim is to show that evolutionary trees, our modern representations of the single Natural System, are also examples of another class of historical representations which may be called «trees of history». As such they can be profitably studied, from both theoretical and practical perspectives, in conjuntion with other trees of history such as genealogical diagrams of language evolution and of manuscript descent. By putting evolutionary trees in the context of other trees of history we will be better able to see the many similarities that tie together the entire range of the historical sciences.

Higher taxa as systems rather than classes

The ontological status of higher taxa has attracted some attention in the recent systematic literature, and Ghiselin's distinction between classes and individuals is often expressed in this literature as a distinction between *classifications* on the one hand, and *systems* or *arrangements* on the other (Griffiths, 1974; Ax, 1987; de Queiroz, 1988; Minelli, 1993; O'Hara, 1993). A classification is a collection of classes each of which contains elements or members. The only important relationship among the elements of a classification is the relationship of inclusion: class A may contain class B, or it may be contained within class B, or it may be independent of class B entirely. In contrast to a classification, a system is an integrated, connected whole that is not made up of classes, but is instead made up connected parts. In a system there are many more relationships among the parts than simple inclusion. There are, for example, positional relationships: parts are not simply components of larger parts, they may also be to the left or right, to

the north or south, earlier or later, above or below other parts within the system.

We can understand the distinction between classifications and systems more clearly if we contrast a map (as a system) with a geographical classification. It would be possible to construct a classification of places in Europe, with «Europe» as the largest class, including Italy, France, Germany, Spain, England, Ireland, and so on. Included under the heading «Italy» in this classification would be Milan, Rome, Bologna, Venice, and Naples; under the heading «England» would be London, Cambridge, Liverpool, Oxford, and Sussex; and so on. But if this classification of places is all we know of geography, then we do not know a great deal. We do not know whether Rome is north or south or east or west of Milan; we do not know whether Oxford is north or south or east or west of London. This is because the classification expresses only relationships of *inclusion*. We may contrast a geographical classification of this sort with a geographical map, which is an integrated whole: a system. A map of Europe will communicate not only relationships of *inclusion* – that Milan and Rome are both within Italy – but also *positional* relationships in geographical space: Milan is north of Rome, and Oxford is west of London.

IDE'E D'UNE ECHELLE
DES ETRES NATURELS.

L'HOMME.
Orang-Outang.
Singe.
QUADRUPEDES.
Ecureuil volant.
Chauvefouris.
Autruche.
OISEAUX.
Oiseaux aquatiques
Oiseaux amphibies.
Poissons volans.
POISSONS.
Poissons rampans.
Anguilles.
Serpens d'eau.
SERPENS.
Limaces.
Limaçons.
COQUILLAGES.
Vers à tuyau.
Teignes.
INSECTES.
Gallinsectes.
Tenia, ou Solitaire.
Polypes.
Orties de Mer.
Sensitive.
PLANTES.

Tenia, ou Solitaire.
Polypes.
Orties de Mer.
Sensitive.
PLANTES.
Lychens.
Moisissures.
Champignons, Agarics.
Truffes.
Coraux & Coralloides.
Lithophytes.
Amianthe.
Talcs, Gyps, Sélénites.
Ardoises.
PIERRES.
Pierres figurées.
Crystallisations.
SELS.
Vitriols.
METAUX.
DEMI-METAUX.
SOUFRES.
Bitumes.
TERRES.
Terre pure.
EAU.
AIR.
FEU.
Matieres plus subtiles.

Fig. 1 - The Scala Naturae or Chain of Being, from Bonnet (1745). Bonnet's original figure is a single folding column. This Chain of Being cannot be reduced to a classification without loss of information, because it represents a system of relationships more complex than simple inclusion.

The distinction between classifications and systems or map-like arrangements is important because classification, as a distinct intellectual activity, has been overemphasized by many writers on systematics and its history. Many systematists of the past, especially the reflective ones, did not see themselves as constructing classifications, but rather as reconstructing a large particular object they called the Natural System (O'Hara, 1993), and for these workers the Natural System was a rich and multi-faceted idea, far more complex than any classification could possibly be. Consider, for example, one of the earliest images of the Natural System: the image of the Scala Naturae or Chain of Being (Lovejoy, 1936). Figure 1 shows an eighteenth-century representation of the Chain of Being, drawn by the entomologist Charles Bonnet in 1745. The information conveyed in this systematic arrangement cannot be reduced to a simple classification without loss of information, because the arrangement depicts not only relationships of inclusion but also positional relationships along the chain: «Oiseaux» does indeed contain many taxa which are not enumerated, but in addition Oiseaux is *above* Poissons and *below* Quadrupedes.

As the diversity of life became better known in the late eighteenth and early nineteenth centuries, systematists came to realize that the Chain of Being was an inadequate representation of the Natural System, and a great variety of more complex representations were developed and put forward (Stevens, 1982, 1984; Barsanti, 1988; O'Hara, 1988a, 1991). The quinarian school of systematists led by William Sharpe Macleay (1819-21) and William Swainson (1836-37), for example, argued that the Natural System is held together by interlocking relationships of affinity and analogy, and that these relationships displayed numerical regularity. Arguing against the quinarians, Hugh Strickland (1841) and Alfred Russel Wallace (1856) represented the Natural System as an irregular map-like entity (Fig. 2) held together by affinities only, affinities that in Strickland's view could sometimes be circular or loop-like.

With the acceptance of the principle of common descent, the notion of the Natural System was converted from a system of ideal affinities to one of physical genealogy (Darwin, 1859: 485). Almost as soon as he became convinced of the truth of the theory of descent, Darwin began to sketch evolutionary trees in his notebooks (Darwin, 1987: 177-180), and the only diagram in the *Origin of Species* itself is Dar-

Fig. 2 - «Map of the Family Alcedinidae», from Strickland (1841). Relationships of affinity connect each genus, and a «Scale of Degrees of Generic Affinity» appears in the lower right corner. Although none are shown here, Strickland believed it was possible for chains of affinity to double back on themselves, forming a loop.

win's well-known representation of an evolutionary tree. Very soon after the publication of the *Origin*, evolutionary trees began to appear in the general systematic literature, and their history between 1859 and 1900 is very complex. The elaborate phylogenies of Ernst Haeckel are among the best known (Oppenheimer, 1987), but many other authors drew trees also (Figs. 3 and 4) and there was much discussion of the methods of phylogenetic reconstruction (Reif, 1983; Stevens, 1984; O'Hara, 1988a, 1991; Craw, 1992; Darwin, 1993: 379-380). It became clear to some systematists at this time, for example, that only shared innovations could count as evidence of common ancestry, and that shared retentions (today called ancestral character states or plesiomorphies) were phylogenetically uninformative (Mitchell, 1901; O'Hara, 1988a; Craw, 1992).

Fig. 3 - A phylogeny of birds, from Huxley (1868). Like many systematists of his time, Huxley published tree diagrams but did not explain in detail the procedure he followed in constructing them.

Around 1900, however, interest in phylogenetic reconstruction began to flag, and as «biologists focused ever more intently on problems of organic function they transferred their allegiance from the ideal of historical explanation, the critical support for all who had studied organic form and transformation, to the promise extended by the experimental investigation of vital processes» (Coleman, 1977: 160). This shift in interest was not universal (Craw, 1992), but it was widespread (Allen, 1975; Zuckerman, 1976; Coleman, 1977; O'Hara, 1988a, 1991). Historical approaches were denigrated as «speculative» (T. H. Morgan in Mayr, 1982: 542) for much of the century, and it was not until the widespread acceptance of cladistic analysis, beginning in the 1970s, that phylogenetic reconstruction attained prominence again.

Trees of history

Let us now consider evolutionary trees in their other intellectual context, as examples not only of diagrams of the Natural System, but also as «trees of history». During the very decades when Lamarck was offering his first speculations on the transformation of species and Lyell was laying the foundations of modern historical geology, scholars in the field of comparative philology were sketching the outlines of a new historical science of language and literature. Although the development of philology in the late 1700s and early 1800s was complex (Pederson, 1931; Aarsleff, 1967; Burrow, 1967), modern-day linguistic historians often point to a statement made by the

Fig. 4 - The evolution of the tubinarial birds, from Forbes (1882). The meaning of the circles and the positions of the genera are not explained in Forbes's text.

English jurist Sir William Jones as the traditional starting point of their discipline. Jones was one of the first Europeans to learn Sanskrit, the classical language of India, and he noticed a number of striking similarities between Sanskrit on the one hand, and Greek and Latin on the other. He concluded that these similarities were much too remarkable to have arisen by chance, and that no philologist could examine all three languages – Latin, Greek, and Sanskrit – «without believing them to have sprung from some common source, which, perhaps, no longer exists» (Jones, 1786). The historical study of this family of languages, which came to be called Indo-European and which stretches from Ireland to India, continued at great speed in the early 1800s. The first genuine tree diagram of the history of Indo-European (and of any family of languages) was apparently published around 1800 (Auroux, 1990), but linguistic trees of history didn't really become widespread until the 1850s, even though the concept of historical families of languages had been clear for some time by then. František Čelakovský, a professor of philology at Prague, published a genealogical diagram of the Slavic languages in 1850 (Fig. 5; Priestly, 1975), but it was the German philologist August Schleicher – who had spent time in Prague and may been influenced there by Čelakovský (Holm, 1972) – who finally popularized the use of tree diagrams in historical linguistics through his widely-read publications (Hoenigswald, 1975; Stewart, 1976; Koerner, 1982, 1987; Priestly, 1985).
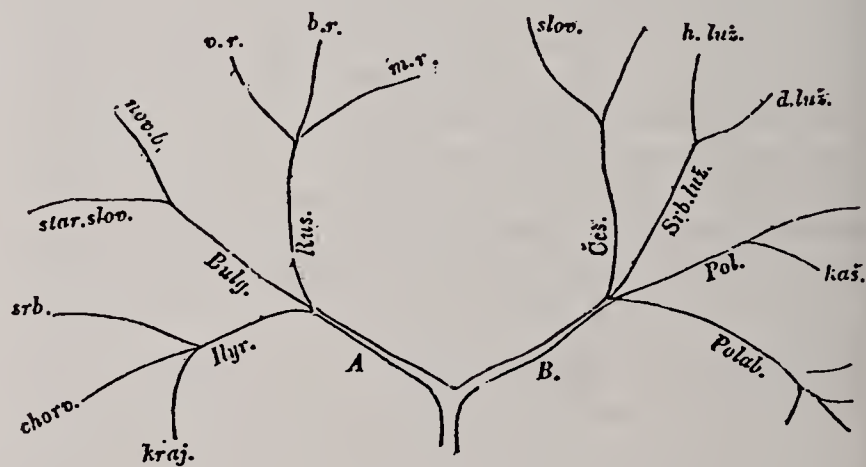
Fig. 5 - A family tree of the Slavic languages by František Čelakovský, published posthumously in 1853. Čelakovský's work may well have influenced August Schleicher, whose own genealogical diagrams have often been regarded as the first trees of language evolution (Priestly, 1985).

The historical study of languages was only one of the tasks of comparative philologists, however; the other was the study of the history of written texts. Most works of ancient literature do not exist today in

copies written by the authors themselves — rather, they are known from copies of the originals, and copies of those copies, often made over a period of hundreds of years and with varying degrees of care. Philologists who specialize in the study of texts are faced with a very specific problem: given ten or twenty or a hundred copies of the same text, all of which differ at different points, how can we determine the exact words of the lost original? The answer is that we can determine the original of the text by reconstructing the tree — or as manuscript scholars call it, the *stemma* — of the copies that now exist. The idea of an ancestral text represented today only by its varying descendants had been clear to manuscript scholars for a long time, but as was the case in systematics and linguistics, the first actual illustrations of manuscript stemmata do not appear until the early 1800s. The first published stemma appears to have been that of Carl Johan Schlyter (Holm, 1972), and it appears in 1827, fully formed like Athena from the head of Zeus. Schlyter and his collaborator Hans Collin had been commissioned by the King of Sweden to research the history of medieval Swedish law, and they made an exceptionally comprehensive study of all the medieval legal documents then known. Many of these documents were multiple copies of original texts that had been lost, and in one such case, in order to «make the relationship all the clearer between the codexes now described», wrote Schlyter, «containing in whole or in part the text of the Västergötland Law..., we have attempted to present their affinities, as far as we could determine them from mutual agreements and differences, in a kind of family-tree» (Fig. 6; Collin & Schlyter, 1827, translated by Holm, 1972: 51-52). Very shortly after Schlyter's tree was published, a series of other manuscript stemmata appeared in rapid succession. Carl Zumpt published a genealogy of the known copies of Cicero's *Verrine Orations* in 1831, and Zumpt's stemma was followed by stemmata drawn by Friedrich Ritschl in 1832, and by J. N. Madvig in 1833. Holm (1972) has reproduced all of these along with several other early stemmata.

As we saw in the case of systematics, after the publication of the *Origin of Species* there was a great burst of tree-making, and much discussion of phylogenetic theory. This same period — the late 1800s — was similarly a golden age of historical philology. Linguistic and textual scholars did an extraordinary amount of work reconstructing the details of the evolutionary history of the Indo-European languages during these years (Pederson, 1931; Morpurgo Davies, 1975; Hoenigswald, 1990), and establishing the original texts of Classical and Medieval authors through the reconstruction of manuscript stemmata (Timpanaro, 1981; Reynolds, 1983). It did not escape notice at the time that the goals of the new natural historians and the goals of the new historical philologists were similar in many respects (Hoenigswald & Wiener, 1987; Hoenigswald, 1990). August Schleicher, for example, published on *Die Darwinsche Theorie und die Sprachwissenschaft* (Schleicher, 1863), and his work caught the attention of Ernst Haeckel as well (Maher, 1966; Koerner, 1981, 1983). And like the systematists, the philologists interested in tree reconstruction quickly recognized that only shared innovations could be used as evidence of common ancestry (Hoenigswald, 1990).

In another remarkable parallel to systematics, however, interest in many of these large-scale problems
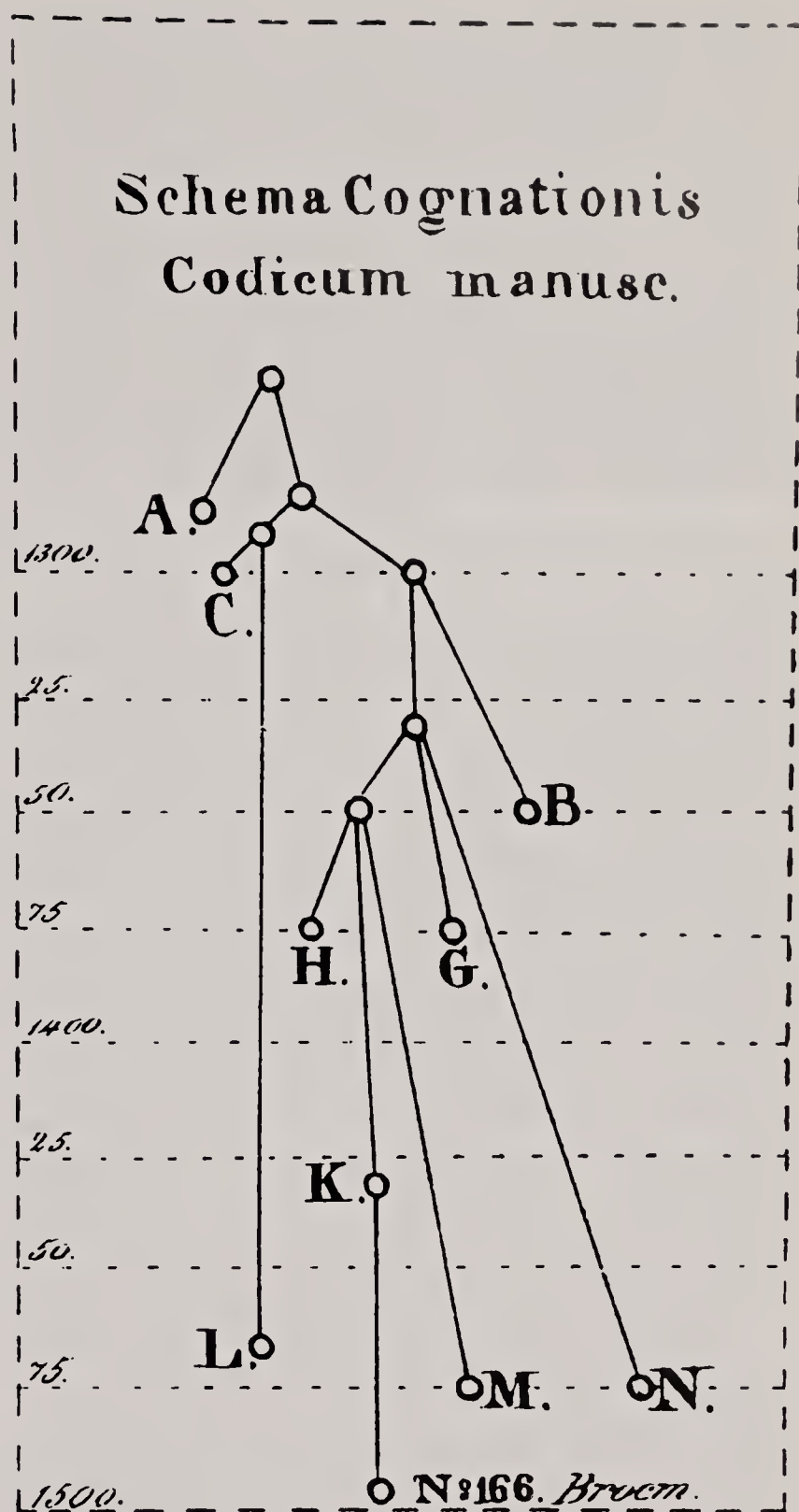
Fig. 6 - A stemma of several copies of the Västgöta Law, drawn by Carl Johan Schlyter (Collin & Schlyter, 1827). The vertical axis represents absolute time, the interval between each dotted line being fifty years. The similarity of this diagram to Darwin's evolutionary tree in the *Origin of Species* is striking, but apparently coincidental.

of historical philology began to wane around the turn of the twentieth century. Many manuscript scholars came to believe that horizontal transmission of readings between manuscripts — called «contamination» in stemmatics — was so widespread that any hope of reconstructing true stemmata was in vain. And linguists began to distinguish between what they called diachronic or historical studies of language on the one hand, synchronic or structural studies of language on the other, and began to regard synchronic, structural linguistics as the most «scientific» approach to their field. Much of linguistics since 1900 has been profoundly ahistorical, almost completely turning its back on the achievements of the nineteenth century (Haas, 1966; Anttila, 1989).

But systematics has re-historicized itself in the last thirty years, and there is reason to hope that the same thing may happen in linguistics and textual studies as well, and it may happen with some cross-disciplinary help from systematics. Some valuable interdisciplinary forays have been made in recent years (Hoenigswald & Wiener, 1987; Flight, 1988; Lee, 1989) and these hold much promise. A collaboration I began in 1991 with a textual scholar who is interested in the application of computers to stemmatics has also generated much interest, and our application of cladistic analysis to the history of manuscript traditions has met with considerable success (Fig. 7; Robinson & O'Hara, 1992, in press; O'Hara & Robinson, 1993).

Conclusion

One of the first scholars to study the interrelationships of the historical sciences was the polymathic British philosopher William Whewell, who was born just two hundred years ago, in 1794. Whewell coined the term «palaetiology» for these sciences, and offered geology, philology, and archeology as examples. Had Whewell become an evolutionist he surely would have included the historical science of systematics in the group as well. The palaetiological sciences, Whewell realized, cut across many conventional disciplinary boundaries, including even the boundary between science and the humanities. And yet all of these sciences «are connected by this bond; – that they all endeavour to ascend to a past state, by considering what is the present state of things, and what are the causes of change» (1847: 638). The reconstruction of trees of history is one of the common themes of the palaetiological sciences, but they share many other themes as well, such as the principle of uniformitarianism, which has been applied not only in geology but also in linguistics (Johnes, 1843; Christy, 1983; Naumann, et al., 1992). Whewell's term «palaetiology» never attained the currency he had hoped it would during his lifetime, but in our own day, as the ahistorical tenor of the mid-twentieth century recedes into the past, the term may be due for a revival. Not since the nineteenth century have Whewell's insights rung so true:

> As we may look back towards the first condition of our planet, we may in like manner turn our thoughts towards the first condition of the solar system, and try whether we can discern any traces of an order of things antecedent to that which is now established; and if we find, as some great mathematicians have conceived, indications of an earlier state in which the planets were not yet gathered into their present forms, we have, in pursuit of this train of research, a palaetiological portion of Astronomy. Again, as we may inquire how languages, and how man, have been diffused over the earth's surface from place to place, we may make the like inquiry with regard to the races of plants and animals, founding our inferences upon the existing geographical distribution of the animal and vegetable kingdoms: and thus the Geography of Plants and of Animals also becomes a portion of Palaetiology. Again, as we can in some measure trace the progress of Arts from nation to nation and from age to age, we can also pursue a similar investigation with respect to the progress of Mythology, of Poetry, of Government, of Law... It is not an arbitrary and useless proceeding to construct such a Class of sciences. For wide and various as their subjects are, it will be found that they have all certain principles, maxims, and rules of procedure in common; and thus may reflect light upon each other by being treated together (Whewell, 1847: 639-640).
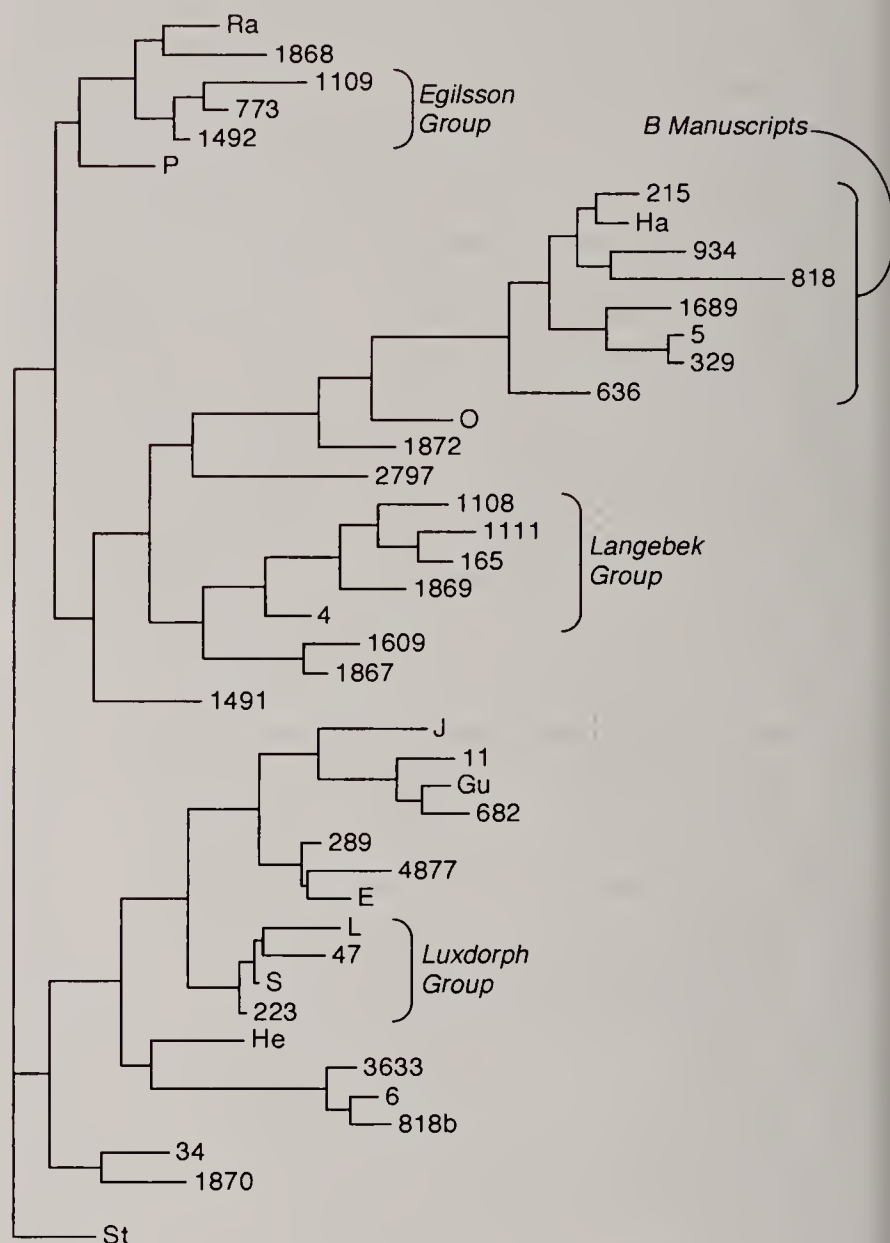
Fig. 7 - A stemma of the Old Norse narrative *Svipdagsmál*, from Robinson & O'Hara (1993, in press). This stemma was produced with the cladistic analysis software PAUP (Swofford, 1991), and it is very similar to the stemma produced by Robinson alone using traditional non-cladistic means (Robinson, 1991). This tree was generated much more quickly, however, thereby allowing the textual scholar more time for critical study and analysis of the result.

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Topological classification: onto- and phylogenesis

Abstract — Here a topological approach is used for the description and analysis of biological morphogenesis. Treating biological structures as topological subjects results in a more adequate description of biological form dynamics than the traditional geometrical description, as topology studies the most general properties of spaces. Moreover, apart from extending of descriptional possibilities the new methodology reveals a topological dependence and topological limitations of biological morphogenesis. Traditional anatomical language is translated into a topological one. Principles and schematics of topological classification of biological form dynamics in ontogenesis and evolution have been elaborated. An evolutionary pattern for the topological shape of animals as well as a scheme for the phylum Echinodermata is constructed.

"Dans la conception axiomatique, la mathématique apparaît en somme comme un réservoir de formes abstraites — les structures mathématiques; et il se trouve — sans qu'on sache bien pourquoi — que certains ascpects de la réalité expérimentale viennent se mouler en certaines de ces formes, comme par une sorte de prédaption.
Il n'est pas niable déterminé; mai c'est précisement en les vidant volontairement de ce contenu qu'on a su leur donner toute l'efficacité qu'elles portaient en puissance, et qu'on les a rendues susceptibles de recevoir des interprétations nouvelles, et de remplir pleinement leur rôle élaborateur".
L'Architecture de Mathématiques - N. Bourbaki, 1948.

For centuries mathematics and biology developed almost independently, although an amazing regularity of biological forms is undoubtedly related to a unitary harmony of the world. In spite of this fact the importance of mathematics is not completely understood by biologists, who sometimes reducine it to an apparatus for statistical treatment of experimental data. This inadequate perspective prevents one from seeing the farthest horizons of mathematical studies. However, physicists realized a long time ago that after the development of an adequate model of any physical phenomenon, i.e. a model enabling one to do precise calculations and predictions, the mathematical structure of the model reveals new properties of the simulated phenomenon. Although it may sound paradoxically, studies of inner mathematical structure of the model may alter our concepts of the real process. This study also provides an extra proof of the well-known idea of N. Bourbaki that some aspects of experimental reality seem to fit some mathematical structures as if due to a kind of preadaptation. This study shows that formulating known biological notions using a new mathematical language relating them to other concepts has some explanatory force.

The naturalists always devoted most of their activities to description and classification of objects of study. Biologists developed a specific system to describe living forms and their transformations in development, but in spite of common features of their descriptions depend on personal interpretations not having completely regular features. Biologists also traditionally use geometrical language to describe the shape of organisms and cells, and the dynamics of form in ontogeny and evolution. However topological language is necessary and more adequate for such description (Listing, 1847; Thompson, 1917; Needham, 1936; Waddington, 1940; Raven, 1959; Thom, 1969; Presnov, Isaeva, 1985; Isaeva, Presnov, 1990), since topology deals with the most general properties of spaces as mathematical subjects. Moreover, topology enables us to analize a transition from local parameters to global ones; it is directly connected to the rather old embryologist's idea concerning an integration of parts and local parameters in an embryo (Driesch, 1894; Child, 1941; Wolpert, 1969). The spatial-temporal integration of individual development can be explained to a certain degree by topological constraints controlling the morphogenetic processes in our physical space; topological properties of the space are reflected in topological form dynamics during ontogeny. So we can discuss the topological determination of individual development.

The topological description of morphogenetic patterns in ontoqeny and phylogenesis is have proposed, attempting to use mathematical terms strictly describing various phenomena such as inhomogeneities, detuning processes and all process of establishing differences during development. For example, the developmental potential of the ooplasm clearly shows that it is not homogeneous object and the problem is not the origin of this heterogeneity, but also it retention and transformation in development. It appears that the ooplasm's inhomogeneities are stable figures, representing topological mechanisms that control morphogenesis.

To see how topological notions may apply to morphogenesis consider the popular description of rubber band with drawings of various configurations upon its surface. Which parts of these configurations would remain unchanged if one stretches the rubber in an arbitrary way without tearing it apart? Evidently that the size and the values of angles and curvature will vary (during such deformation) as they do in development and in evolution. But in the topological

description of living systems we should also account for the topologically invariant characteristics. The power of topology lies on operating on such properties in analytical form.

A translation of anatomy into topological language

The external shape of an organism, as the shapes of its organs and tissues, are modeled by smooth closed surfaces. The morphogenesis of most multicellular animals may be represented through topological modification(s) of their epithelized surfaces. A layer of epithelial cells is characterized by morphological and functional connectivity, closeness of its surface in the intact organism and apical-basal (outer-inner) anisotropy of the cellular sheet. This allows to neglect the thickness of the cellular layer, considering epithelia as smooth, closed, oriented two-dimensional surfaces. The connectivity of an epithelial layer during epithelial morphogenesis (by folding etc.) is ensured by the system of specialized cell-to-cell contact – fulfilling the function of integration of cells and their cytoskeletal systems into a united morphological and functional entity. Through such prerequisites one can develop a combinatorial approach modeling the morphogenesis of a whole organism.

Let us apply a theorem of elementary topology to the spatial organization of epithelial layers: any closed surface in three-dimensional space is homeomorphic to a sphere with a given number (p) of handles. The sphere with p handles sets a class of homeomorphic surfaces of the genus p. So long as there are no topological surgeries (breakings and glueings) of epithelial sheets the genus of the surface p is a topological invariant and any detailed geometry (curvature of surface, angle values) is not essential. According to the proved theorem the closed surfaces of the *genus*

$$p = 0, \quad p = 1, \quad p = 2, \quad \dots$$

give a full topological classification. An example of such a surface is the *sphere* to which *p handles* are *attached.* Usually the topological handles in biological objects are represented «through channels» such as the digestive tube, i. e. – any through channel or hole in an organism is topologically equivalent to handle. Then topological morphogenesis in the development of a living organism (as in evolution) is given by series of topological modification (*surgeries*) of closed surface. For example, the surface of an egg, the outer surface of blastula or early gastrula as well as the bodily surface of an adult coelenterate are surfaces of genus 0, that is homeomorphic to a sphere. The epithelial surface of an embryo or a larva with a through intestine tube (having both oral and anal openings) such as the outer surface of an annelid or nematode worm is a surface of genus 1, topologically equivalent to a sphere with one handle attached or to a torus (Figure 1).
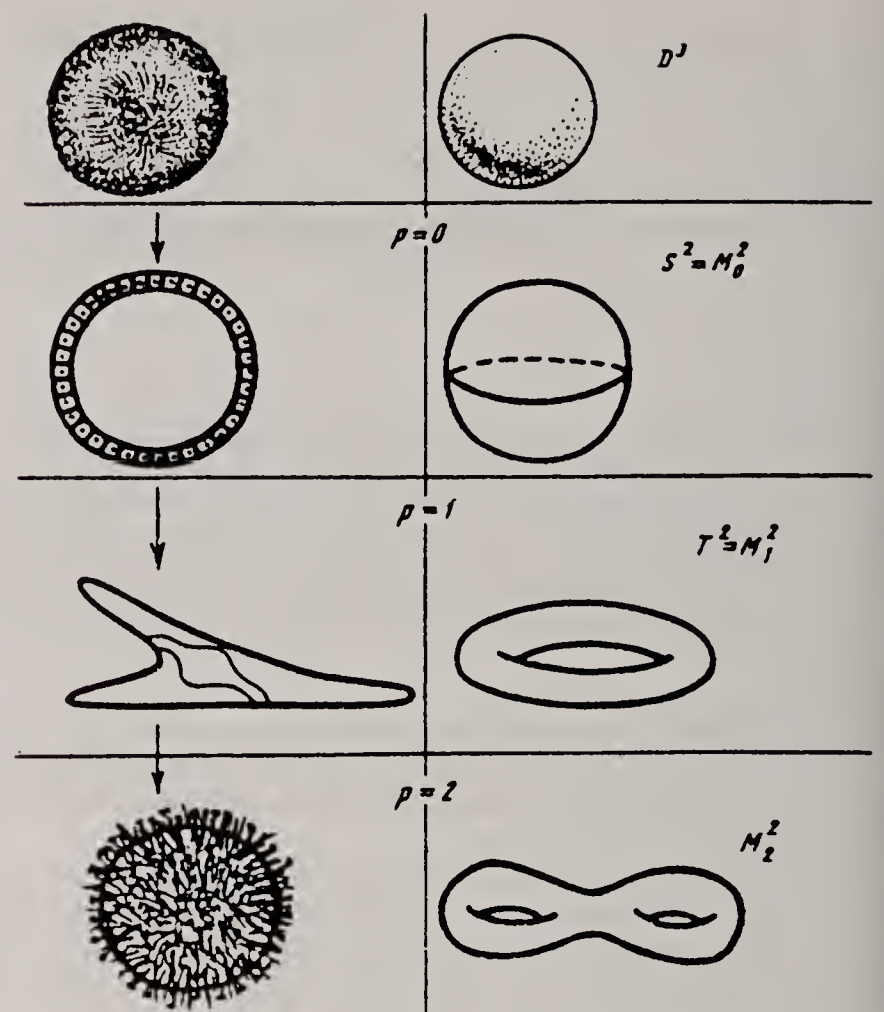
Fig. 1 - Topological models of biological shapes. Left column: stages in the development of sea urchin: egg, blastula, larva, definitive shape. Right column: 3-dimensional ball, 2-dimensional sphere (genus 0), torus (genus 1), closed surface of genus 2.

Viewing topologically the digestive tube is an outer surface of an organism is unusual for biologists (1). The contents of the digestive tract are undoubtedly part of the external mediun flowing through an organism; the intestine epithelium is a boundary tissue – between the internal medium of an organism and the outside medium; epithelial cells function as bordering, absorbing and conditioning the external medium elements.

The bodily surface an organism with one through channel besides the digestive tube is a surface of genus 2, topologically equivalent to a sphere with two handles.

Through channels of the respiratory system are also filled with an external medium, so that the surface of the respiratory system too may be considered as outer surface of an animal. Coelomic cavities opening outside by coelomoducts with unidirectional flow of coelomic fluid from the cavity are physiologically better, but not completely, isolated from the external medium; the content of coelomic fluid in marine annelids, mollusks and echinoderms is similar to that of marine water. In general the epithelial surface of an organism having n through channels is homeomorphic to the sphere with n handles – i.e. is the translation of anatomy into topological language.

(1) According to Prof. A. Minelli's opinion, in some parts of biology this notion is well accepted: in parasitology the category of parasites living in the gut is clearly separated from the category of the true endoparasites living within the tissues.

Topological modifications of epithelial surfaces in ontogenesis

"Digestive channel, arterial system (including the heart), the central nervous system (including brain) appear as simple tubular structures. The nature machines them as a glassblower".
On Growth and Form - D'Arcy Thompson, 1917.

During development in most animals the surface of an organism, say, an epithelial envelope of an organism, undergoes topological modification or sequential modifications (surgeries) of the closed surface, changing the topological genus of this surface, except for those in which the definitive state is a genus 0 surface (coelenterates, flat worms). As in higher animals the epithelial surface of an embryo or larva with a through intestine tube is a surface of genus 1 (torus) during development the genus of the surface (so called «spherical surgery») is inevitably transformed: $(p=0) \rightarrow (p=1)$. This transformation is a transition from a blind archenteron to a through intestine tube and is usually realized at the gastrula stage of development by means of an appearance of another opening opposite the blastopore; the blastopore (or primary mouth) will be the definitive oral opening in Protostomia or anal opening in Deuterostomia. So the through intestinal tube arises by the break through of the mouth opening (in Deuterostomia) or one anal opening (in Protostomia) into the blind archenteron.

Animals having surface of genus 1 as adults (for instance, round and annelid worms) undergo in ontogenesis only the transformation from sphere to torus:

$$(p = 0) \rightarrow (p = 1).$$

The ontogenesis of animals with the genus of outer surface 2 (echinoderms and mollusks - see below) inevitably undergo two transformations:

$$(p = 0) \rightarrow (p = 1) \rightarrow (p = 2).$$

In other of protostomions and deuterostomions with higher order adult state the surface genus $1 + 2n$ (see below) the following transformations take place:

$$(p = 0) \rightarrow (p = 1) \rightarrow (p = 1 + 2n).$$

Thus during embryogenesis the surface of an organism undergoes sequential topological (i.e. spherical) surgeries, changing the topological genus of their surface. These surgeries are local phenomena, whereas its genus is a global characteristic. Topological surgeries changing the connectivity of germ (embryonic) layers are also possible; different types of topological surgeries modifying spatial organization of epithelial sheets in ontogenesis have been described earlier (Presnov, Isaeva, 1985). Topological modification of the connectivity of germ layers results in a separation of additional closed spherical surfaces from preexisting ones, for example during neurulation in chordates. Spatial organization of the organism of an evolutionary advanced animal may be represented topologically as an outer epithelial envelope (or shell) of certain genus p embracing a numer of inner closed epithelial surfaces, that are embedded inside the outer envelope. However the modifications of connectivity do not change the topological pattern of this outer surface shell (Figure 2).
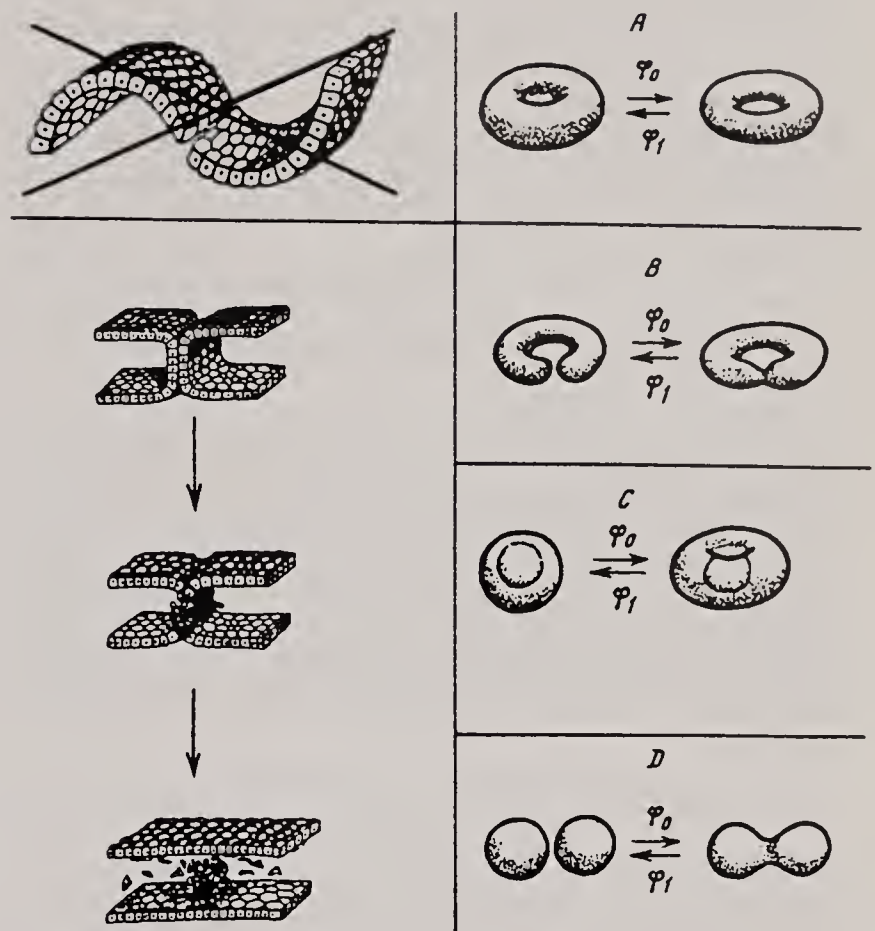
Fig. 2 - Modifications (surgery) of topology during embryonic pattern formation. Left column: local aspect of surgeries; Right column: global aspects of surgeries. φ_0, φ_1 - surgeries. A_{φ_0} — oral plate rupture; A_{φ_1} — obliteration of branchial clefts; B_{φ_0} — obliteration of choroid fissure; B_{φ_1} — separation of somites from splanchnotome; C_{φ_0} — mouth breaking into blind archenteron; C_{φ_1} — neurulation; D_{φ_0} — fusion of two heart anlagen, formation of a single body cavity when the sheets of lateral plate fuse; D_{φ_1} — enterocoel mode of the formation of the mesoderm.

The topological surgeries in epirhelial sheets become realized locally at the cellular level; cellular mechanisms of the epithelial are sheet disintegration, cell migration, cell adhesion and epithelization, but any topological surgery always is global topological modification of biological form.

Evolution of topological forms

Plant organisms as a rule do not have any obligate through channel; all the variety of forms in the plant kingdom is created by pure geometrical complication without topological modifications [2]. Although there are various perforations of plant body in some species, most plants have the genus of the surface equal to zero ($p = 0$). The topological form poverty and rigidity in plants probably is restricted on the cellular level by immobility and fixed position of cells and cellular associations.

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[2] For example, the stomata of higher plants may open into common cavities, but these parenchymal cavities are irregular and not epithelized. We consider as topological handles only epithelized through channels.

In the animal kingdom, however, cell mobility, specific cell adhesion and morphogenetic cell death ensure the creation, destruction and variability of supracellular associations as a topological variety of form in evolution.

The analysis of topological modifications of the closed epithelial layers covering the outer surface «envelope» of a developing organism (formed both by the external epithelium and by the intestinal epithelium too) is also applicable to consideration of topological organisation of the bodily surface in evolution. And here also the topological modifications changing the genus of the surface are important as modifications of connecticity don't change topological pattern of bodily surface.

The most primitive of recent multicellular animals, Placozoa, have a surface of the body without any through epithelized channels that is homeomorphic to sphere.

Poriferes have numerous channels penetrating all the body and connecting the spongocoel and choanocyte chambers with the external medium. From the topological point of view the genus of the surface in sponges is indefinite and extremely high. Such a peculiarity in topological organization of Porifera confirms the data and conclusions of comparative morphology on sponges as a special branch in animal kingdom.

Coelenterates (Cnidaria) and flat worms (Turbellaria) are characterizing in ground plan by a blind intestine which is opened by a mouth functioning also as an anus. As any blind invagination do not change the topological genus of the surface, its value is 0 too. Thus the form of above types of animals did not proceed above the level of a sphere ($p = 0$) although in separate representatives of these types numerous evolutionary attempts to acquire anal opening and consequently the through intestine have been observed: the sole pore of hydra, pore channels of intestine in some Turbellaria, intestine pores of actinia, pores of the circular channel in some jellyfishes. None of these openings are homologous to the anal opening of higher Bilateria. Few representatives of flat worms have one or several anal pores.

The appearance of a through gut, instead of a blind one is a topological modification of great evolutionary importance, since the external medium flows through it resulting in better utilization and conditioning of the medium, and better digestion and absorption of its elements.

In animals of many taxa the gut is the only any other through channel. The differentiation of many organ systems proceeds through blind, often branching, invaginations, obviously giving various possibilities for the evolution of organ system. Mollusks and echinoderms have achieved a next stage of topological organization of the surface since, besides the digestive system, they also have a second through channel due to increased integration of the coelomic system. In mollusks the through channel opening outside via two coelomoducts and coelomopores results from the fusion in to one (of pair of coeloms).

Most echinoderms exhibit a second through channel due to presence of ambulacral ring channel opening outside by one canal (see below). Such pattern of ambulacral system is topologically homeomorphic to torus of sphere with one handle.

Thus biological evolution in mollusks and echinoderms results in a second through channel, but this way of topological modification seems to lead the evolution into a dead end, it is not used by higher representatives of Protostomia or Deuterostomia animals developing another system of through channels. The next level of topological organization in the animal kingdom is achieved due to development of through channels of the respiratory system: tracheal system in higher terrestrial arthropods ([3]) and gill clefts in chordates. The system of paired tracheal tubules connected laterally (in arthropods) or the system of through paired branchial clefts (in chordates) results in a surface, which in topological terms is homeomorphic to the sphere with $2n$ handles, i.e. having the genus $2n$ (n is number of respiratory openings).

The creation of through respiratory system is the topological modification of the bodily surface which results in better utilization of oxygen from outside medium (air or water) flowing through the organism, conditioning of the medium flow and more intensive metabolism; it can be considered as the next step in evolution. The acquisition of the through respiratory system correlates with the development of the most advanced morphological and functional organization — among protostomes in insects, among denterostomes in chordates.

Thus a parallelism of topological and functional modifications in evolution of both protostomes and deuterostomes is obvious: a transition from the sphere in the topological sense ($p = 0$), that is an organism without a digestive cavity or with a blind gut, to a tube or in topological terms the torus ($P = 1$), an organism with through digestive tract, and subsequent transition from the torus by adding an even amount of channels (handles) of the respiratory system to the surface of genus $p = 1 + 2n$. The acquisition of the surface of the genus 2 may be considered as a blind branch in evolution both Protostomia and Deuterostomia. The evolution of the topological form of the surface in animal kingdom may be shortly expressed in the following summing up schematics (see also Figure 3):

$$
\begin{array}{ccc}
 & p = 1 + 2n & \\
p = 2 & \uparrow & \\
 & \nwarrow\uparrow & \\
 & p = 1 & \\
 & \uparrow & \\
 & p = 0 \rightarrow p = N &
\end{array}
$$

The general similarity or even identity of evolutionary and ontogenetic form modifications makes it possible for us to develop a unified topological classification of biological forms.

([3]) There are lateral connections or anastomoses between tracheomeres in some Diplopoda and Araneina. In most insect tracheal tubes are connected by a system of lateral and transversal channels (Beklemishev, 1964).
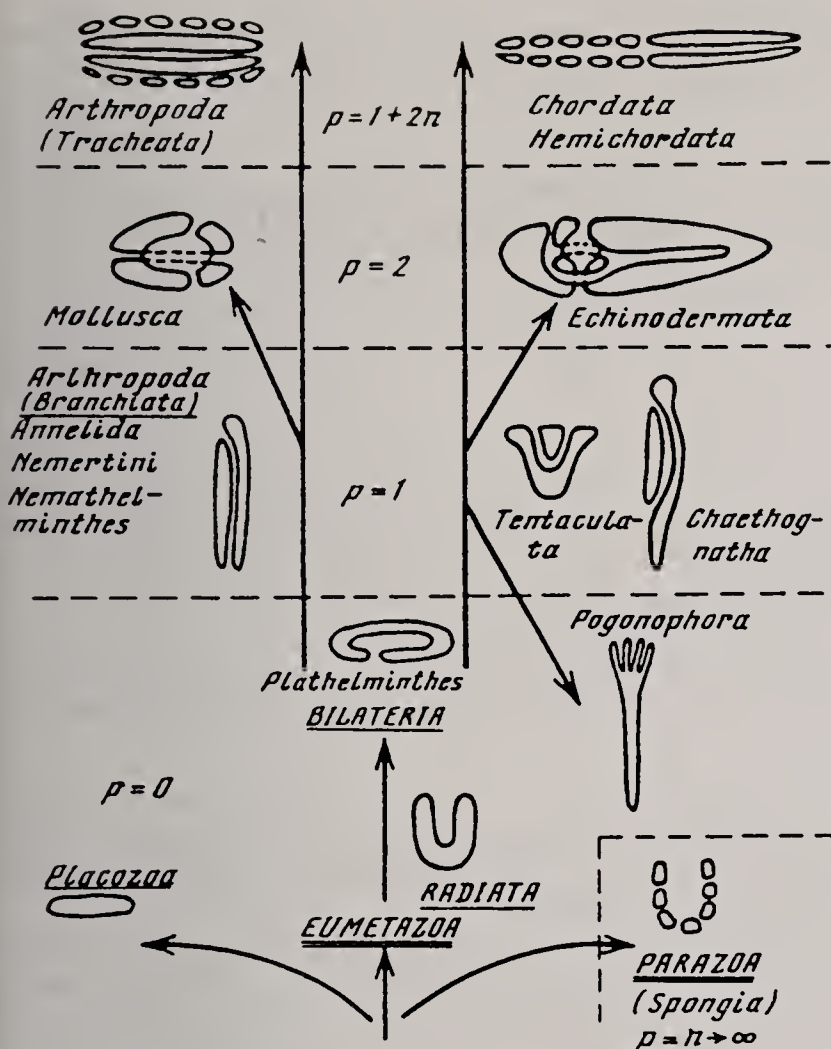
Fig. 3 - Schematics of evolution of topological forms of animals.

A topological classification based on embryonic form dynamics

Although the trend of increasing the genus of surface and the amount of isolated layers in onto- and phylogenesis is obvious, modifications decreasing both the genus of epithelial surface and the amount of closed isolated epithelial layers sometimes occurs in onto- and phylogenesis. Hence the time ordering of modifications should be also taken into account. Since the topological modification (surgery) is canonically related to the hole of the surface, we will order the holes (through channels, or handles) and mark them by C_j. The symbol C_j acquires either the value of 0 or 1 depending on the absence or presence of j-th fundamental hole. After that the set

$$(C_1, C_2, \ldots, C_N)$$

will correspond to any organism. It is clear that the dynamics of above set (word) in animal's ontogenesis would be more complete than the resulting genus of the outer surface

$$p = C_1 + C_2 + \ldots + C_N$$

– classifying characteristics. The usual dynamics of variation of coding word in the majority of animals is

$$(0) \rightarrow (1).$$

However, in animals with embryonic envelopes or specialized larvae, for instance in the annelid worm *Polygordius* we have the following scheme:

$$(0) \rightarrow (1) \rightarrow (0) \rightarrow (1).$$

During embryogenesis of *Peripatopsis capensis* (Onychophora) an amazing bifurcation can be observed:

$$(0) \rightarrow (1,1,1) \rightarrow (0) \rightarrow (1).$$

This mathematical approach to describing of developmental phenomena is convenient and simple; it enables us to give the detailed classification of recent echinoderms.

Scheme for the phylum Echinodermata

The topological genus of the bodily surface of an echinoderm is equal to 2 for the ground plan with through gut and circular ambulacral system opening outside through an additional channel. Now we will take into account also another through epithelized holes appearing and vanishing during embryogenesis. We will consider and distinguish the functional value of each through channel. Thereby, we have at hand four types of channels:

gut, ambulacral system, hydropore, waterpores.

The numerical characteristic: C_1 corresponds to absence (0) or presence (1) of the through gut. C_2 – to absence (0) or presence ($C_2 > 0$) of circular ambulacral system opening into outside medium by one (1) or more ($C_2 > 1$) channels; ($C_2 > 1$) also corresponds to presence of anastomoses connecting two rings of the ambulacral system in *Concentricycloidea medusiformes* ([4]). C_3 corresponds to the presence of connection of hydropore with the outer medium by one simple hole (1) or through madrepore plate with multiply pores ($C_3 > 1$). C_4 designates the presence ($C_4 > 0$) of the pores of the sea lily cup.

During planctonotrophic type of development of sea urchins, starfishes, ophiurans and holothurians the genus of the surface of their larvae is $p = C_1 = 1$ (presence of through gut). In cases of lecitotrophia no through channels are observed prior to metamorphosis in these animals or in crinoids. During metamorphosis the through digestive tract vanishes temporarily in planctotrophic larvae. The development of ring channel of the ambulacral system opening outside only through the stony channel (in sea urchins, starfishes, ophiurids, some holothuria) or through five channels (in sea lilies) provides the topological genus of the bodily surface to be equal to $p = C_2 = 1$ or $p = C_2 = 5$ respectively. In the definitive state the most echinoderms have a through gut ($C_1 = 1$), but Concentricycloidea, Ophiuroidea and some Asteroidea are exclusive ($C_1 = 0$). Most echinoderms exhibit a connection of the ambulacral system with the outer medium through multiple madreporite pores ($C_3 > 0$); only in sea lilies is there a

([4]) Concenticycloidea (whose only the representative is *Xyloplax medusiformes*) may be regarded as a class (Rowe et al., 1988) but other evolutionary systematics prefer to treat *X. merusiformes* as highly specialized Asteroidea. Here we represent Concentricycloidea as a separate class (or a separate group of lower rank) of Echinodermata.

system of numerous acqueous pores through the cup surface ($C_4 > 0$) (Figure 4).

Using the system of ontogenetic variations the change of classifying word:

$$(C_1, C_2, C_3, C_4)$$

and definitive values composing its letters we plotted a scheme for six classes of recent echinoderms with the following sequence (see also Figure 5):

Fig. 4 - Topological schematics of ontogenesis in echinoderms. Column I: embryogenesis; Column II: metamorphosis; Column III: definite state.

{ Crinoidea → Concentricycloidea → Holothuroidea → Asteroidea → Ophiuroidea → Echinoidea.
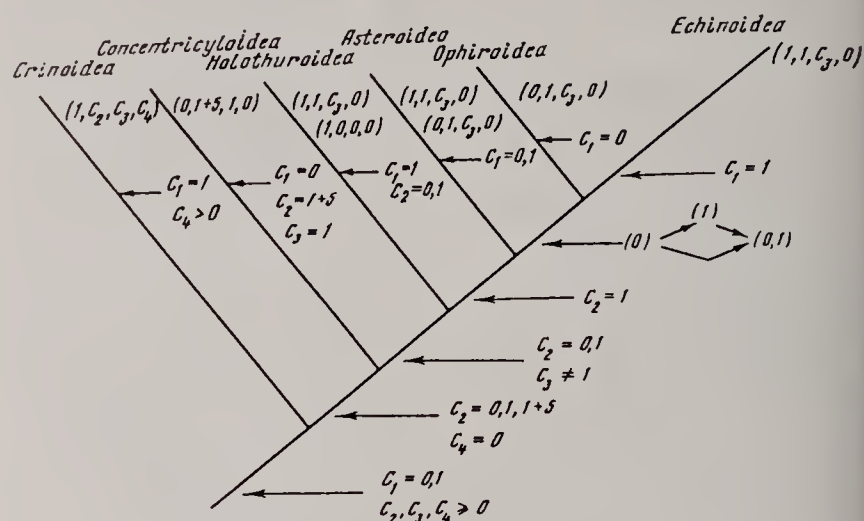
Fig. 5 - Scheme of echinoderms using topological parameters.

The similarity between this topological classification and legitimate zoological classifications proves the naturality of such topological approach which additionally is quite simple.

Thus the analysis of topological form dynamics in ontogenesis may provide additional possibilities in cladistic analysis although the construction of a given scheme based on pure topological characters is only an experiment, as in cladistics many different characters besides the topological ones should be taken in account.

Generally the topological approach gives a new adequate and strict language for description and classification of biological forms and their dynamics in embryogenesis and evolution.

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Francesco M. Scudo

Symbiosis, the origins of major life forms and systematics: a review with speculations

«It is often said that all the conditions for the first production of a living organism are now present, which could ever have been present. But if (and oh what a big if) we could conceive in some little pond, with all sort of ammonia and phosphatic salts, light, heat, electricity, etc., present, that a protein compound was chemically formed ready to undergo still more complex changes, at present day such matter would be instantly devoured, or absorbed, which would not have been the case before living creatures were formed». C. R. Darwin, as in F. Darwin (1887), Vol. II: 202.

Abstract — It is difficult to explain the origin of prokaryotes proper other than through symbioses among «uncoded» proteinoids, on which viruses eventually flourished. Cellular coding would thus have started as a symbiotic enterprise of very diverse viral elements, in which a large variety of codes were at first established in order to prey upon, or parasitize quite diverse proteinoid cells. Prokaryotes proper might have accasionaly merged into chimaers, and so apparently did more complex cells closer to eukaryotes. Nuclear structures proper appear to be of late, multiple and possibly symbiotic origins, connected with regular alternations between the haploid and the diploid cellular phase. These low eukaryotes then acquired diverse endosymbiotes, mostly bacterial, which they permanently retainod as organelles; some of them quite likely originated from distinct symbiotic events, involving much the same symbiont. A common triplet code was eventually established among the metazoans and the metaphytes. Their cellular specializations were made possible by the gender differentiation of the haplophases, that took place in many eukaryotic lineages in a few standard forms. In higher metaphytes and seemingly all extant metazoans this haploid gender specialization was then replaced by true hermaphroditism, in turn often resulting in diploid gender. The metazoans continued to form close, physiologically specialized symbioses with algae, fungi and bacteria. A common outcome of bacterial symbioses consisted in transferring to the host's genome some relevant functions of the symbiont, that was then discarded as such. Analogous, radical transformations induced by much the same symbiont on rather different metazoan stocks could have rendered them far more similar, as quite likely happened for the Hyrudinea, the Pogonophora and the Blattoidea, possibly the Cirripedia etc.. Directly «genotypical» symbioses with viruses also remained common especially among the higher animals, whose genomes largely consist of repeated, mobile elements of viral origin. Traditional systematic practices are not well suited to deal with these modes of often multiple origins.

This review deals with theories on origins of major life forms in order to explore possible connections among them and implications for systematics. § 1 will start by touching upon a few examples of reconstructions with restricted aims, mention some of the constraints or problems that ought to be taken into account and finally consider a few treatments aiming at completeness. Based on these treatments, § 2 will sketch a sequence of connected scenarios for the origins of the prokaryotes, the protists, the metazoans and metaphytes (§ 2). § 3 will then examine the very different «tempos and modes» of evolution these scenarios imply, and some of their direct consequences for systematics. More general problems in systematics are approached in the Final Remarks from an historical perspective, also as a way to justify some theoretical premises.

The term «symbiosis» is now being employed with two radically different meanings. The recent meaning, now comon, is to denote any close, often endocellular association, most of which are clearly pathogenic. Symbiosis is, intended here in the traditional sense, to denote bodily associations that are obligatory at least under given conditions, and take place in standardized rather than erratically varying ways. By being standardized, any such association is assumed to benefit at last the «host» even if the precise nature of the benefits is not known. A qualification of symbioses as «mutualistic» is problematic in many cases, of animals in particular (cf. e. g. Nardon *et al.* 1990). Most well understood forms of close symbiosis in animals clearly point, in fact, to a parasitic or predatory first origin, that only involves mutualism in any proper sense as intermediate evolutionary stages. Although common, hereditary associations are not a necessary prerequisite for highly specialized, obligatory symbioses. Thus the luminescent symbiotes of many cephalopodans are highly specialized forms of «wild» photobacteria that remain «extracellular», and are obtained by the host at each generation by infection from free living ones (cf. Pierantoni, 1923, Ruby & McFall-Ngai, 1992).

It is worth anticipating major differences in the symbiogenesis of taxa that clearly affect the very foundations of systematics. The principles and goals of taxonomy and phylogeny mainly stem from comparative anatomy of the vertebrates and other deuterostomians proper. These easily establish full genomic integrations with viruses but only rarely close symbioses with bacteria or fungi, and only in special cases these have major consequences at macroscopic levels. On the other hand metakaryotic protists are

essentially qualified by the nature of their symbioses with different microorganisms. In most metazoans other than deuterostomias algal, fungal and bacterial symbioses are relatively common, and most have major irreversible consequences also at macroscopic levels (e. g. Nardon et al., 1993). As a result, different stocks of most eukaryotes can be rendered more similar by establishing symbiotic bonds with the same microorganism. Ample parallelisms, or convergencies also arise among the metakaryotes from very similar forms of sexual differentiation. As one turns to prokaryotes the quest for common ancestry might prove even more elusive if, as it seems these originated through innumerable symbioses among previously «free» proteic components and, then, nucleic ones.

1) On theories and problems

a) «Popular» theories about origins

Only in the 1920's Oparin and Haldane managed to turn the problem of origins into a socially acceptable topic for discourse. Till the late 1950's this mainly consisted in general arguments for the origins of simple life forms from non-living Earth materials, carried on as if hardly anything was known on the functions of their different chemical components. By the late 1950's it had become clear that DNA was indeed the «universal» carrier of inheritance, as Miescher had claimed nearly a century earlier. Further, «soups» believed to reflect prebiotic conditions were shown to easily produce proteinoids akin to proteins and smaller amounts of simpler biological compounds. Molecular biology then clarified many aspects of life components and of their interactions, among which reverse transcription and the enzymatic and «editing» properties of RNAs are of special relevance to first origins (cf. § 2 a).

Most theories on first origins that are directly based on molecular knowledge concentrate on one of the major components of life — usually RNA or proteins — as if it had a near absolute primacy over other components whose origins are hardly explained. How coding came about is the central problem to which very diverse solutions are offered — e. g. earliest life having been coded by some clay entities, and only much later real genes having «taken over» (Cairns-Smith, e. g. 1985). Assuming that RNA came first seems to be a satisfactory way out of «chicken and egg» problems, but only *in vitro.* Thus it seems impossible to obtain the nucleotides, the building blocks of nucleic acids, through abiotic synthesis. On the other hand «proteins» can easily phosphorylate nucleosides to nucleotides, and simple sugars are «robustly» produced abiotically as are the bases (far more so purines than pirimidines (e. g. Miller, 1993). Even if the building blocks of RNA could have been produced abiotically, their assemblage does not appear likely other than through surface catalysis. Then to energize this assembly, while sparing the final product from the disrupting effects of the same energy, only seems possible if RNA's had an extraordinary tendency to dive as soon as «born». It is even harder to imagine how these RNA's could have survived «on their own», cells being their only known and reasonable-looking support. On the other hand combinatorics would not be much of a problem by reasoning on an «RNA World» in terms of Wright's «shifting balance theory» (e. g. 1970, cf. § 2 a) on very numerous «species» of biomolecules (cf. Eigen, 1987, apparently unaware of the extent his reasoning overlapped with Wright's).

Life having started with membranes might seem an easy alternative to an RNA primacy as these can easily self-assemble in proper conditions also in the form of «microspheres», capable of selective osmosis and doubling, or fusing. This alternative too is often phrased in exclusivistic tones such as the Genesis-mocking «In the Beginning was the Membrane» (Harold, 1986: 168), while not any more complete, or convincing than an «RNA World». Still another way out of concentration and energizing problems would be for life-components having started in bubbles. As both bubbles and wet surfaces are common around ponds, some among the innumerable steps of precellular life might well have taken place in either of these ways.

All along there had also been deep analyses of one or another aspect of origins, with very reasonable answers it considered separately. Thus the theory according to which viruses would have originated from RNA molecules ecaping the control of cells looks as reasonable as its main alternative — i. e. that they came about «alongside with the molecules of life» (in fact the former is a precondition to the latter in the scenario of § 2 a). There are, however, astronomical numbers of combinations and permutations of the answers for all the steps involved, among which it is hard to make meaningful connections and even harder to choose. Thus both «compartimentalization» theory of eukaryotic organelles and that of viruses as «degenerate» prokaryotes might seem reasonable on their own, but it is hard to make sense of both other than by assuming that the metakaryotes come first, and the prokaryotes came from desymbiotyzed organelles. A major premise of the present analysis is that problems of polarity — i. e. a given process appearing about as reasonable as its reverse one — are less likely to arise the larger the set of organisms, or events being considered.

b) Some among the many «facts» a complete theory ought to take into account

Recent, explosive increases in factual knowledge added very different «constraints» to theories on origins, most of which concentrate on bringing about a reasonable prokaryotic «progenote» or on interpreting eukaryotic organelles as symbioses with prokaryotes. Some among the most surprising and apparently more binding such constraints concern timing and physical conditions, to which only rarely sufficient attention has been paid.

For instance it has been firmly established that at least the inner planets originated by stochastic accretion of discrete bodies (e. g. Dones and Tremaine 1993) — i. e. «planetesimals» that are occasionally «double» or comets that could land in one piece or, more likely, break up preceeding impact. Further, though it is not yet clear how, or why, the Earth achieved an orbite very close to the present one about four billion years ago (e. g. Milani 1988) — i. e. only shortly before the first cells appeared. The longer the Earth kept to much the same orbit the better

it «sweptin» any respectably sized body with which it was likely to collide. Collisions, in fact, might have been a primary mechanism responsible of well spaced planetary orbits, with periods far from resonance, out of more chaotic initial ones (Scudo 1993).

Such «accretions» must have had far larger direct physical effects on the atmosphere and dry land than on the *whole* oceanic masses, and still larger indirect effects as through accumulations of snow and ice and their subsequent melting. These physical changes would have mainly affected the more complex forms of animal life, resulting in the simultaneous, global extinction of many animals while plants would get by more easily through spores, or seeds. Then the transformations of life are not, or not only the nearly continuous processes in which many believed, and in which some continue believing in spite of all the evidence to the contrary. Rather, many life forms were suddenly destroyed at times, and each time new «normal» life arrangements came about by re-associating in different ways the survivors, some of which were drastically changed (cf. § 3 c).

The fossil record thus produced shows that prokaryotic-like cells existed for about 2 billion years with hardly a major recorded change. Eukaryotic-looking cells likewise persisted for a quarter to half that long with hardly any noticeable change, before rapidly giving rise to most animal phyla and the early green land plants (cf. Fedonkin, these proceedings). Any reasonably complete theory on origins must then account for these two long periods of stasis, during which disturbancies of cosmic origin were more frequent and substantial than later on.

Furthermore, any theory aiming at completeness ought to also account for «puzzles» such as the substantial variabilities in chemical composition of DNAs and in codes among viruses, and the far lesser ones among the prokaryotes and the lowest eukaryotes. Virology treatises usually justify DNA's chemical variability as a defense from bacterial restriction enzymes, and some DNA variants might indeed have this function. On the other hand, to my knowledge, no sound reason has been given as to why this justification would also apply to *Bacillus*, viruses having *only uracil DNA*. If life had indeed started from a coding «progenote», among other things it would be hard to justify the variability in DNA composition and codes among prokaryotes and low protists.

c) On theories aiming at completeness

Only very few theories on origins aim at completeness and none of them has, or has ever had much following. The oldest such theory by Giglio-Tos (mainly 1900 to 1910) is also by far the most complete, though it deals with the basic features of life only in a simplified way – i. e. much as gravity explains the features of rivers. The amount of labour involved in drawing from gravity any detailed inference about specific problems concerning rivers gives a good idea of the lack of detail in Giglio-Tos' theory, which in turn justifies its standing up in terms of present-day knowledge. Thus GT deals with large combinations of biomolecules, the *biomores*, without specifying their chemical nature or spatial arrangements and just distinguishing between «somatic» and «genetic» ones. Life would have started with very simple molecules capable of doubling by transforming different chemicals from a primeval broth, as well as of changing and transmitting their changes. As suitable biomolecules thus came about, «symbioses» among them would have given rise to simple biomores. Then different, sufficiently advanced biomores would have been forced to associate symbiotycally into simple protocells or *biomonades;* more advanced biomonades would have then specialized their biomores into somatic and genetic ones, as in prokaryotes and organelles. Then nucleated cells would have arisen by symbiotic associations of different, genetically specialized biomonades, as Mereschowsky and others had already proposed (e. g. Khakina, 1979).

Much as it was for Darwin and followers such as Moebius and Cuénot, for GT any form of life under «normal» conditions was, as it still is, bound to others by interactions that often have substantial mutualistic components. Should a parasitic or predatory bond persist long enough undisturbed, among suitable organisms, it would tend to become an «indissoluble» symbiosis. One among GT's most original achievements was a relatively complete theory on the relationships between sexual reproduction and development – i. e. gender would be the pillar of the mechanisms through which vegetative cells can differentiate genotypically, and thus allow for the extended «symbioses» of multicellularity. As this theory incurred in a gross, hardly avoidable «mistake» (Scudo 1994) I shall here consider it in an amended form (§ 2, c), confining its topological features to the Final Remarks.

Only recently have there been reasonably complete attempts to show how life components could originate in the «natural» order of increasing complexity of their synthesis – i. e. «proteins» first, nucleic acids last, fatty acids and sugars in-between. Though full of «it is far from obvious how...», Folsome (1979) is noteworthy by starting from a reasonable protocell not yet coded for; however he gets around the notorious combinatorial problems through random but exceedingly small biomolecules, such as 5 to 7 aminoacid peptides. The remarkable enzymatic and «behavioural» properties of RNA's were discovered mostly later (cf. Symons 1992), radically changing the rules of the game.

The stale «chicken-egg business» alluded to in a) was set in motion again by two remarkable works: Cordón (1990) and de Duve (1991). Different as they are in many respects, these concur with Folsome in assuming that veritable «proteic» cells – rather than just proteinoid membranes – came about before any cellular coding proper. So far, Cordón's pubblished treatments have arrived at the simplest such cells that are still open, vase-like, made up by a layer of proteic beings of a single kind that grow much as do the germinal lines of volvocales or the pyrosomes, with a lipidic layer on the inside. He painstakingly explains why such heterotrophic colonies, saprophytes of autotrophic ones, were forced to evolve veritable cellular behaviours (1990, Vol. 1) and then he examines the early phylogeny of biochemical cycles (1990, Vol. 2, cf. also Scudo 1992a). De Duve's theoretical preferences are analogous to Cordón's on many counts, to the notable exception of cells becoming closed very early, thus making it hard to explain the origin of viruses except than by «degenera-

tion» (cf. § 2a). The sequence of tentative scenarios that follows is liberally based on the treatments by Giglio-Tos, Cordón and de Deuve, aiming to account for «facts» as in b) above.

2) Some «complete» scenarios for origins

a) The rise of the cells and the «genetic takeover»

The precise nature of the earliest, «chemical» steps of life remains to a degree conjectural since the initial composition of the atmosphere is still an open problem (e. g. Kasting 1993). These steps themselves are not problematic, however, since even very simple chemical systems share with present-day life the basic features of self-duplication, «mutation» and «selection» (e. g. Hong *et al.,* 1992), and different life components are synthetized abiotically in a wide variety of conditions (cf. § 1 a). I am thus sketching here a plausible sequence of events starting from diverse proteinoids, primarily globular enzymes, associated in complex systems or, more precisely, *biogeocoenoses.* These relatively complex, non-coded «free proteins» would have been error prone in reproducing, which is hardly problematic since plenty of sequence variations have only minor effects on function, and all reproduced about as inefficiently. Some such proteic being would form different types of «colonies» including heterotrophic, open «cells» like Cordón's (cf. § 1 c), which would provide a basis for symbiotic associations with other, non-colonial «proteic» beings.

According to Cordón the above process would have reached a turning point when the coenzymes in a cell type included the building blocks of present-day RNA, or alike compounds no longer found in it. Some short «Ur-RNAs» capable of relatively error-free replication would have formed easily, at first with no function other than storage-transport. Then these Ur-RNAs would have then developed other useful functions, such as repair of proteic components or physical support for their production. The physiologies of these Ur-RNAs might have then become akin to the still poorly known ones of viroids and virusoids. By being easily transmissible among the still open cells, some such Ur-viroids would have spread from their native cell types to others as mild predators-parasites, suited to acquire all kinds of symbiotic functions.

As cells thus kept increasing in complexity, the next turning point would have consisted in some viroids starting to build capsids out of cellular aminoacids, thus developping primitive codes and larger chromosomes. The greater power of dispersal and more complex physiology thus achieved would have allowed them to be really virulent on some hosts. Greater dispersal would also have resulted in more horizontal exchanges among different viral stocks tending to homogenize their RNAs, quite likely initially variable also in chemical composition. Some cell types would have reacted to ever increasing parasitic loads by closing up, thus accelerating the symbiotic adjustment of the entrapped «viruses». Ohnishi (e. g. 1990) provides direct evidences for coding having originated as a collective, symbiotic entreprise of distinct RNA organisms.

Alongside the above process some viruses would have started to «prey upon» RNA components more efficiently by differentiating forms of nucleic acids for the sole purpose of replicating their chromosomes, namely into Ur-DNAs. The uracil DNA of the *Bacillus,* viruses might represent an obvious step in this process which, by taking place near-independently in different viral and cell lineages, would have resulted in DNAs chemically far more variable than those now extant. In this scenario many, possibly all variants in DNA chemical composition would be remnants of this initial variability rather than modifications of an originally homogeneous DNA, in part retained by assuming functions such as defense from restriction enzymes. Notice how the two major theories of viral origin usually presented as alternative (cf. § 1, a) here become complementary — i. e. RNA molecules that «escaped the control of cells» would have been the starting point in the evolution of coding.

From a variety of coding mechanisms and DNAs, mastered by symbionts-parasites of cells, further evolution of coding would have been a biocoenotic process at a still more extended, more collective level. Any one viral lineage could undergo direct genetic exchanges with others and it would be subjected to diverse selective pressures also from different host cells, in which it quite likely played different roles. Any such virus, originally parasitic on a cell type, could have slowly turned into its symbiote and then be incorporated into its chromosome, perhaps with quite different functions than in other cell types. Somewhere along these processes of symbiotic specialization, the establishment of reverse transcriptases would have made coding easier also for proteic components proper of cells. Cellular coding might thus have started by «copying» proteic components into messenger RNAs and then retrotranscribe them to DNA, as proposed by de Duve (1991). «Genetic take over» of chemical information in any one cell type would have soon resulted in a single «main» chromosome, as the only manageable reproductive arrangement.

In turn, establishing a single cellular chromosome opened the way to a complete, efficient «genetic take-over» as in the extant eukaryotes. For long this might have been a major adaptive goal among cells that no longer shared, or exchanged coding functions to the extent they did while still open — i. e. they did so only occasionally through new viral symbiotes as plasmids or sexual processes. Quite likely symbioses between prokaryotic lineages also took place rarely, such as between a poorly motile and a highly motile one, and the chromosomes of the «partners» soon merged. The extant variability in the chemical composition of DNAs and in codes among viruses and prokaryotes would then reflect the level of homogeneization achieved at the outset of eukaryotic evolution, as further reduced by differential extinction. These processes would have taken place through much the same selective effects of the struggle for life as in the «biogeocoenoses» of multicellular ornanisms — i. e. involving both selection and chance, both within and among populations (cf. Wright, e. g. 1970 and § 3 c).

Quite likely code homogenizing only resumed on a wide collective basis in the evolution of the metakaryotes. DNA and coding uniformity thus eventually resulted among the metazoans and the metaphytes, whose chromosome complements are

made up in substantial proportions by repeated, mobile «viral» elements.

b) The origin of the eukaryotes

The eukaryotes are characterized by their cytoskeletons, by mostly very similar chromatin arrangements and by a variety of nuclear organizations – i. e. micronuclei, macronuclei and nuclei proper, with different modes of division. The higher ones (Metakaryotes or S80) also posess a variety of organelles not found in the lower ones (Archeozoans or S70). Reasonably detailed reconstructions tend to agree on basic issues in the evolution of the the Archezoans (e. g. de Duve 1990, Cavalier-Smith 1990) and on distinctive metakaryotic organelles – notably ribosomes, plastids and peroxisomes – having originated from symbioses with prokaryotes.

Far from clear, on the other hand, are origins of microtubule-associated motors such as in the axonemes of cilia and flagella, in mitotic and meiotic spindles and other processes of mechanical transport. These microtubules and motors might all be due to much the same machinery of symbiotic origin, as suggested by direct biochemical or structural evidence (e. g. Margulis *et al.* 1990) as well as by many eukaryotes «reabsorbing» their cilia or flagella during cell division. This might contrast with many reasons why the evolution of the S70's would not have been accompanied by any symbiotic event (Cavalier-Smith 1990). Further, reasonable explanations for the origins of microtubules and their associated motors might also quite directly account for a number of eukariotic taxa lacking cilia and flagella, or having flagella only in the sperm.

A satisfactory explanation of all these evidences might thus be far more complex than often assumed – e. g. the «inner» motor machineries of eukaryotes having originated from a symbiotic event prior to the evolution of most other S70 features, while the metakaryotic cilia and flagella originated from different symbiotic events with prokaryotes lacking close, known relatives. It is hard to choose among many plausible reconstructions of such events so long as the biochemical evidence is still as incomplete as at present (e. g. Walker and Sheetz 1993), end detailed ultrastructural evidences are still scattered (e. g. Engelhardt *et al.* 1993).

All eukaryotes seem to have primitively undergone an alternation between a haploid and a diploid cellular phase, still retained in different forms by most of them.

In many protists the diplont is dormant and highly protected, carrying the population through adverse conditions and then giving rise to four haplonts. The syngamic processes through which two haploid cells produce the zygote or analogous set-up (dicaryonts in fungi, diplokaryonts in microsporidians, e. g. Canning 1988) are mediated by very different adaptations. In many low protists syngamy is achieved by haplonts of uniform size (isogamy) through sequential modifications of their behaviours – e. g. agglutinating as a start. Their most primitive sexual specializations consist in many genotypic differences called poles, each pole favouring syngamy with a different one. In more advanced forms syngamy within the same polarity is altogether prevented with various consequences – e. g. only one of the uniting cells passes on a given organelle (cf. e. g. Hurst and Hamilton 1992). The most avanced forms of these evolutionary sequences consist of only two poles (bipolarity).

In a few low protists, however, syngamy takes place among cells that do not appear to have any polarity differentiation but widely differ by size in a continuum. Here syngamy always occurs between two cells with at least some size difference, the smaller one distinctively behaving «as male», the larger one «as female» (relative sexuality).

Except in some of their lowest representatives, the gametic phase of the metakaryotes is specialized into sperm and egg cells (spermatic nuclei, oospheres); in many forms without cilia or flagella, such as red algae and nematods, sperm and egg cells are close in size. These specializations, collectivively denoted as oogamy, often look very similar. They apparently evolved innumerable times among unicellular protists, often directly deriving from bipolarity – i. e. one of the poles splits into four or eight smaller cells just prior to syngamy while the other looses its flagellum(a) (e. g. Bacci, 1965).

On the other hand it is far from clear whether, and in which cases, oogamy directly evolved from relative sexuality, altogether bypassing isogamy and polarity (e. g. Scudo 1973, cf. also further evidence from *Iriconympha*).

From its distribution, oogamy appears being an essential precondition for the diplophase to become substantially dominant over the haplophase in multicellular eukaryotes. Thus most if not all algae first evolved multicellularity in «identical» forms in the two phases, the diplophase slowly becoming dominant only after becoming oogamous. This dominance reaches extremes, as in the Fucales, where the spores are retained on the mother diplont, soon entering gametogenesis. At variance from algae, in green land plants a substantial dominance of the diplophase was only achieved after a marked cellular differentiation, as in ferns.

On the other hand it seems that most, if not all the ancestors of metazoans had developped multicellularity from the outset only in the diplophase, altogether lacking an independent haplophase (cf. e. g. Scudo 1973).

The operation of natural selection seems to justify in a simple, general way that all organisms with a dominant diplophase are oogamous. It is easily shown (Haldane 1924, Scudo 1975) that individual selection for a genetic variant operates on a sexually undifferentiated haplophase «about» twice as strongly as in the diplophase. This statement roughly describes the results of approximate analytical models showing that selective contests about dominance are strongly biased in favour of a sexually undifferentiated haplophase. On the other hand, in the same contests a variant affecting only one haplont gender would «play about even» with one affecting the diplophase. The gender differentiation of the gametes can obviously provide various direct advantaged besides those to be examined below, such as size dimorphism to easily result in more efficient unions in demanding circumstances (Scudo 1967). Since a low gametic dimorphism is far from rare both among protists and animals – even higher ones such as some crustaceans (Baccetti, e. g. 1985) – it is not per se indicative of gender specialization.

c) Gender, development and the origins of the metazoans and the metaphytes

As hypotesized by Giglio-Tos (cf. § 1, c) the most primitive, general function of gender would be to allow cellular specializations also other than sexual – i. e. «epigenetic» modifications in ontogeny could only revert to a state close to the initial, zygotic one through syngamy between gametes of different gender, or *amphimixis*. Cellular specializations could only evolve through such epigenetic modifications though these might no longer be necessary for development at subsequent stages. Here different particularizations of these assumptions – now supported by direct evidences such as methylation, including sexual imprinting in the vertebrates, cf. e. g. Jablonka *et al.* (1992), Jablonka (1994) – shall be explored through direct evidences and plausible inferences on mechanisms. To this end, first recall how haploid, gametic gender always appears being under strict control of constitutive genomic differences – i. e. a major diallelic or an heterochromosomal segregation in all known instances of bipolarity, anisogamy and oogamy. At least in some bipolar forms – e. g. *Schizosaccharomyces pombae* (Arcangioli 1992) – reversible gender marking or «imprinting» is also evident *at the level of chromatids*, rather than at that of whole haploid genomes as in some diploid systems.

In hermaphroditic metazoans either sperm or eggs are usually produced usually in different parts of the body, or at different times, as is also the case for monoecious Bryophytes and for micro and macrospores in monoecious metaphytes – i. e. all these forms lack segregational mechanisms for gametic or sporal gender.

Diploid gender consists in individuals being specialized to produce different proportions of sexually differentiated gametes, or spores, up to complete separations of these sexes or *gonochorism* in animals. These specializations too are usually connected *somehow* to constitutive genomic differentiations, though in no known case they appear to be *strictly determined by a single mechanism.*

Thus «environmental» sex determinations of metazoans also have, as a rule, at least some hereditary variability for the threshold of response to the gender-triggering stimulus. In the classic case of *Bonellia viridis,* for instance, most larvae exposed to a mature female settle on her as parasites thus becoming males; if not so exposed they settle on the ground, becoming females. A small proportion of larvae, however, are «true males» that never settle on the ground, and soon die if unable to find a female host (cf. Bacci 1965). To the partial exception of heterochromosomes, the effects of dialleic mechanisms for gonochorism are subjected to all kinds of modifications by external conditions, as for producing intersexes or reversals of the genotypic sex according to temperature or age of the egg at fertilization. As a rule gonochorisms through heterochromosomes are far less dependant upon conditions of growth as far as the «primary» sexual phenotype is concerned, while the whole sex phenotype often remains substantially «plastic». In the latter case *whole haploid genomes* are often epigenetically gender-marked, as for sperm imprinting in mammals. At least in humans the differential utilization of the paternal and of the maternal complemens in ontogeny has been directly, macroscopically evident since long (e. g. Weismann 1904).

On the other hand a strict determinism of the whole sex phenotype seems only possible through a complex balance between the heterochromosomes and autosomal loci, acting in different ways through their maternal and syngamic (zygotic) effects (e. g. Cline 1993). It is thus safe to infer some general, necessary links between gender differentiation and mechanisms of epigenetic inheritance, regardless of whether known at the molecular level, that explored as an Appendix.

3) Systematics and the diverse «tempos and modes» in evolution

The scenarios of § 2, a) are analyzed here in terms of traditional and symbiotic phylogenetics, with reference to data such as introduced in § 1, b). As both such phylogenetics substantially differ from contemporary usages (cf. e. g. Minelli, these proceedings), it will be useful to first recall their basic principles and terminology. In traditional phylogenetics an assemblage of lineages that originated from some common ancestor constitutes a taxon. This is qualified by a set of characters or character combinations at a given epoch, and it is said to be monophyletic if the common ancestor belongs to the taxon as so qualified. Unless meant to imply that a taxon is artificial, in traditional phylogenetics the term «polyphyletic» is usually accompanied by some restrictive qualification – e. g. «the *modern* reptiles are likewise definitely polyphyletic» (Schmalhausen 1968: 289, my emphasis).

In symbiogenetic systematics, on the other hand, as a rule a taxon is qualified by the establishment of an obligatory symbiosis. If this symbiosis originates only once between given representatives of two taxa, the symbiogenetic definition of the taxon coincides with the phylogenetic one. However a taxon, say C, symbiogenetic of A an B (A U B), often originates at distinct places or times, through distinct representatives af A and B, say A1 U B1, A1 U B2, A2 U B3 etc., as due to some common external pressures on A and B such as an «infectious» spread of the symbiote. If such a taxon is sufficiently distinctive – or so is just the symbiote as for chloroplasts – its multiple origins by no means imply that it should be regarded as artificial.

These prescriptions straightforwardly apply to close algal, fungal and bacterial symbioses, all of which have been infrequent, lasted very long as such and always had major, irreversible consequences (cf. e. g. Pierantoni 1923, Buchner 1965, Smith & Douglas 1987 and the Final Remarks). On the other hand attempting to strictly apply the same rule to other symbioses could make systematics «impossible» – e. g. viral symbioses in the metazoans where they are frequent and can easily differ within a Linnean species, or the same viral genome might be shared by the nuclear complements of very distant species. Here the traditional prescriptions of symbiogenetic systematics will be followed only to the extent they would not force giving up major, established taxonomic terminology or general, useful canons in systematics (cf. Simonetta, these proceedings).

a) On prokaryotes and their origins

Should the scenario in § 2, a) be anywhere close to truth it would necessarily imply that the prokaryotes and organelles are intrinsecally, highly polyphyletic, to an extent which is not easy to ascertain. These would in fact represent any number of lineages – most likely not just very few – out of innumerable lineages of non-coding cells, as originated by distinct symbiotic events. Coding would also result from very many symbiotic events, at times involving different coding agents with analogous functions. Further, in the process of homogenizing codes and DNA's among protocells, some proteic component could have been easily transferred from a lineage to another, or any two lineages might have symbiotically fused, and thus be misleading about proteic ancestry in ways that are hard to disintricate.

Turning to the *tempo* of pre-cellular and cellular evolution, notice how the scenario in § 2, a) easily justifies a fast rise of cells looking prokaryotic in the record, while only partially coded or not at all. Then the near-stasis of such cells for about two billion years (Ga) would be mostly an apparent one, corresponding to the evolution of cellular coding. Such an early establishment of cells would have been possible since biochemical evolution took place quite rapidly up to the establishment of free-living proteinoid entities, mainly since these had very short life spans. Further, the evolution of free protenoids was most likely ruled by the fast chemical changes in a medium still very far away from its near-equilibrium, as eventually reached mainly through photosynthesis. This changing chemical composition would have imposed strict conditions only on the functions of catalytic agents, quite regardless of their precise structures or sequences.

Due to the generally scarce sequence specificity of the early, free-living proteinoids, natural selection would have been rather inefficient on them. Selection would also have had slow and with relatively loose effects on colonies of proteinoids and on non-coded cells, since these were likely to have somewhat more precise forms of reproduction than free proteinoids, but their life spans would be far longer. Early cellular evolution would also have been slower than «free» proteic one by being mostly caused by chemical changes life was producing, and these tended to occur at a slower pace than earlier. Further, early cellular evolution quite likely took place through collapses of complex, previously established biocoenoses of different cell types, to be replaced by novel ones. Previously, it was rather the matter of chemical cycles being modified by a novel enzyme which got established, more often than not just changing the status of some old one rather than eliminating it (see agaion, Cordón 1990, Vol. 2 and de Duve 1991). During early cellular evolution the still substantial and frequent impacts (cf. § 1, b and c below) could easily heat up most of the oceanic masses and evaporate part of them without resulting in major, global extinctions of simple, hardy proteic beings, widely distributed and highly variable. Then cellular evolution might have been so slow also, or mainly since it was not speeded up by sudden mass extinctions of exogenous causation.

Even a primitive, partial coding of cells would have allowed natural selection to achieve far stricter results than on non coding ones. Coding, however, is not likely to have much speeded up cellular evolution, since selection would operate upon more complex, longer living cells. Most likely early prokaryotes were even less sensitive to physical conditions of life than their extant representatives (cf. Fedonkin, these proceedings) so that extinctions among them would still be mostly caused by the ever slower chemical changes they produced, notably oxygen accumulation, No wonder, then, that it might have taken about two Ga for protocells to master coding mechanisms. Incidentally, infering parentage among prokaryotes and organelles through components of their coding machineries might well mislead as to their ancestral proteic parentage. Thus the evident diphylety in the rRNAs of modern Gram positives (van de Peer *et al.*, 1994) might well reflect an ancient phyletic divergence after these had become established or, rather, an originally diphyletic, symbiotic establishment of rRNAs.

Il prokaryotes and organelles had indeed all diversified from a coding «progenote» it would be hard to explain haw this could have evolved in very few hundred million years, or why its descendants so much differentiated their codes and also the chemistry of their DNAs before giving rise to the eukaryotes. Rather, the notion of a progenote might just derive by applying the «normal» assumption of monophyly to the origin of cells where it would just pose severe, most likely spurious problems – e. g. the evolution of chromosomes as dealt with by Eigen (e. g. 1987) through a precarious balance between «hypercycles» and «compartments». Much current theoretical literature is struggling for better solutions to this problem that does not arise in the scenario of § 2 a) just because, as a rule, any one «viroid» had to «fit» into different cells through somewhat different means.

b) Symbiosis and the evolution of the Eukaryotes

As pointed out in § 2, b) the eukaryotes share some basic biochemistry, cytoskeletal features and some sorts of nuclei. Among the lower ones even DNA composition, codes and chromatin organization are still quite variable (cf. e. g. Rizzo, 1991 for the dinoflagellates), suggesting that also their nuclei might have had multiple origins. Much the same might well apply to the presence versus absence of cilia or flagella, as a primitive feature probably connected to the evolution of nuclear division (cf. § 2 b, if unicellular, the haplophase could be spared from this loss). Regardless of the precise extent to which the metakaryotes might be regarded as «ancestrally polyphyletic» their organelles might have more different origins than directly evident – i. e. «the same» organelle might have had multiple origins – as apparently the case for chloroplasts (e. g. Cavalier-Smith, 1990). Also a variety of endocellular symbiotes appear to have levels of integration akin to organelles while departing from them for their more restricted localizations, as for the Gram negatives that are essential for the survival of all cockroaches.

The peculiar «epixenosomes» of the ciliate *Euplotidium itoi but for lacking a nucleus* have all the appearence of microsporidians (Rosati *et al.*, 1993) and thus support the view that nuclei were multiple acquisitions, rather likely late ones through symbioses. Though somewhat controversial (see again Fedon-

kin, these proceedings), the fossil record points to the eukaryotes not showing major, recorded innovations for about one Ga prior to rapidly giving rise to most or all metazoan phyla. Then this «stasis» too could well agree with the reasoning in § 2, c) in being just an apparent one, corresponding to the symbiotic origins of the nuclei, then of the metakaryotes and to the evolution of their haploid sexual specializations.

If analogy with bryophytes and lycopods applies (cf. the Appendix) the original haplont sex system might have been homogenized in a number of vascular stocks while keeping the haplophase dioecious. If so, the metaphytes might still be regarded as monophyletic in the sense of originating from related Charales stocks. The metazoans too are likely to derive from distinct homogeneizations of the haploid sex system in multicellular stocks but, as far as one knows, they might well be polyphyletic in the more basic sense of having had rather different, unicellular protistan ancestors. More detailed knowledge of cellular components and distinctive motory organelles, such as the «missile-type», might reveal such ancient parentages, so far elusive.

In principle the problem of single versus multiple symbiotic origins might be more precisely approached for metazoan taxa, as in the classic example of roaches, termites and mantids that still remains controversial (cf. e. g. Handlirsch 1908, Grassé and Noirot 1959, Buchner 1965, Scudo *et al.,* MS). The same problem seems more easily amenable to a precise solution for the pogonophorans, since this «phylum» is represented by two rather diverse taxa, the Vestimentifera and the Perviata, each of which is rather homogeneous. While solely known through Perviata adults, pogonophorans were regarded as deuterostomians of uncertain affinities, having unique features such as an apparent digestion through tentacles (e. g. Becklemishev, 1969, I: 394). The quite different vestimentiferan juveniles confirm the close affinity of pogonophorans to anellids, already maintained by Livanov and Porfirieva (cf. Becklemishev, 1969, II: 214). Their main difference from anellids is evidently due to the bacterial symbiotes filling, and much enlarging the cells of their guts (e. g. Smith & Douglas 1987) — i. e. in the smaller Perviata this has a much reduced lumen, which appears being altogether eliminated in the Vestimentifera. The distinctive pogonophoran traits thus seem having separately originated in two anellid stocks, by moving to unusual habitats where both domesticated the same sulfide oxidizing bacterion. The relationships among the Vestimentifera, the Perviata and their anellid ancestors are still far from clear, however, since they share «telling» traits both with polychaetes and oligochaetes (e. g. the axonemic structure of the sperm, cf. Baccetti 1985).

c) On extinctions, plant and animal evolution and their physical causes

The metazoans and the metaphytes appeared when the physical conditions on Earth were already fairly close to the present ones. An atmosphere with much the same chemical composition as now was undergoing regular weather fluctuations, to which there were superimposed erratic glacial periods, occasional bursts of tectonic activity and the effects of impacts, progressively more rare and smaller on average (cf. § 1, b). As individuals, metazoans and metaphytes tend to be more sensitive than protists to physical conditions of life (cf. Fedonkin, these proceedings) though often able to resist short term disturbances in terms of propagation, as through resting eggs and seeds. A far more precise fossil record than for protists (cf. again Fedonkin) shows that, especially among animals, major rediations tended to follow mass extinctions, some of which are sudden or have large «instantaneous» components.

Much recent evidence points to boundaries between eras and lesser epochs as often coinciding in time with, and somehow be caused by major impacts (cf. § 1, b). Such would be the multiple ones on the southern tip of the Gondwana (Gondwana II) corresponding to hardly separable craters over a thousand miles radius in South Africa and South America. This was quite likely due to a comet breaking into several pieces prior to impacting, though the pieces migh thave acted mechanically as a «single impact» causing the Gondwana to break up. While impacts leave hardly questionable signatures such as microtektites and nanodiamont sprays, many objections keep being risen against their causative roles on «coincident» border extinctions. These objections largely stem from considering only the direct effects of impacts — i. e. tsunamis, fires, atmospheric cooling and acid rain from dust — as well as from reasoning on species rather than on biocoenoses (cf. below). Less direct interpretations of impact effects, much as in Vernadky's tradition, can easily turn such objections into revealing insights on less direct modes of action. Thus consider glaciations, that hardly fit Milankowitch's otherwise excellent predictions of climatic periodicities, and seem to be best interpreted as the result of uplifting tendencies and their subsequent reversal by glacial accumulation (Kostitzin 1934, also in Scudo and Ziegler, 1978). Let us briefly see how this mechanism could easily «magnify» the effects of impacts (Scudo 1993a).

In a non-glacial epoch, cooling due to the dust of a large impact is likely to result in a rapid, massive accumulation of snow, perhaps too short-lasting to turn into true glaciers. As temperature climbs back to normal, this snowmass melts quite rapidly, even if melting is not speeded up by the subsidences it might cause. During glacial accumulation, cooling from an impact could easily reverse an uplift still under way, or much speed up a subsidence that had just started. Jointly with the warming up that follows, the meltdowns of preexisting glaciers and of the recent snow accumulations would thus be much faster and massive than «normally», and nearly synchronized. Needless to stress how the effects of such anomalous snow-ice accumulations — their very rapid melting in particular — are likely to be far more devastating for many organisms, in many habitats, than the cooling that caused them. The K-T boundary appears to well fit this kind of reasoning by corresponding to a relatively modest impact — though probably much larger than previously thought, namely a crater about 300 kilometers in diameter (Sharpton *et al.,* 1993) — preceeded by two-three million years of unusually strong telluric activities such as the Deccan basalt floods (Basu *et al.,* 1993).

The interactions between cosmic and terrestrial processes are still poorly understood in general, save perhaps for the effects of major early impacts on the

atmosphere (cf. again Kasting, 1993). Whichever their causes, however, the Earth surely underwent numerous, sudden catastrophic changes (e. g. Ager 1993) and one should try to understand how and why these affected evolution. To begin with, notice how the characteristic forms of biocoenoses tend to all be exceedingly persistent in the absence of major disturbances, while any sufficiently global disturbance tends to jointly eliminate most such forms (large, specialized animals in particular). The collapse of any one «harmonic fauna», then, is primarily related to its complexity and specialization, much in the same sense that a complex machine is more likely to either work well or not at all than a simpler one. No wonder, that the prominent, highly specialized components of rich, long established faunas tend to either persist or disappear jointly, as can be easily realized also *a priori* through mathematical models such as Volterra's (cf. Scudo and Ziegler 1978).

Such extinctions might thus easily include whole, long established taxa, particularly of large, specialized, compulsorily cross-breeding animals that cannot change fast, if at all, nor survive in small patches or at low densities (cf. the «limited variability» within taxa in the Final Remarks). The reverse also holds in such conditions — i. e. animals that are smallish, phenotypically plastic etc. will all tend to rapidly change to some degree. At the extreme, a sufficiently «plastic» lineage forced to colonize a new, nearly desertic habitat, might give rise to «hopeful monsters» that can survive by having no enemies, and are more likely to enter new symbioses than in normal conditions. The «wrong» genes of these monsters can be subjected to directional individual selections of intensities that are not possible otherwise (e. g. Haldane 1953). Still more relevant, perhaps, through a partially stochastic operation selection within populations can be faster and «cheaper» than in mass conditions, and result in a substantial selection among populations that magnifies and spreads far more «creative» results (Wright, e. g. 1970). Thus improved upon, «lucky monsters» might soon be able to withstand the modest competition from poorly adapted outsiders that would start moving in.

As a possible example consider barnacles, as assessed by Darwin to represent different stocks related in ways he did not succeed ascertaining, nor did others later on (cf. Ghiselin, these proceedings). It was recently suggested (Alessandrello et al. 1992, Scudo 1993) that barnacles derive from sandy bottom crustaceans related to thylacocephalans, rather than directly from pelagic crustaceans as Darwin had proposed. If so, of their two «metamorphoses» (e. g. Darwin 1851: 103) — both quite likely caused by sudden changes in sea level — the one to pupa would represent the switch to sandy bottom growth resulting in «thylacocephalans», the one to adult the final switch to a solid substratum. Each such switch of substratum might have renderd more alike diverse lineages ancestral to barnacles, as well documented in other cases (cf. b above and the Final Remarks). Then barnacle ancestry might be so difficult to untangle due to their multiple origins as dwellers of hard bottoms, possibly of soft ones as well. Incidentally if Darwin (e. g. 1851: 12) was correct in assessing the cement as being the same adaptation in all, very different barnacles, and a unique one, this striking coincidence might well be justified by distinct symbiotic origins in ancestral lineages, involving the same microorganism (cf. again the Final Remarks for well documented cases).

Final remarks

Many points in this review depart from current fashions and, to lesser degrees, also from more firmly established positions. So far tentative phyletic reconstructions were justified mostly through plain common sense as for «viruses» and the evolution of coding — i. e. being the simplest organisms with coding machineries akin to «higher» ones, most likely viruses played a central role in their origin. Here I shall allude to a sample of theoretical foundations that were mostly subsumed so far, in the guise of an historical sketch of systematics, that emphasizes the tensions between common practices and infering the history of life.

One might well start with Lamarck, according to whom discovering «the order of production of living beings» should be the «first and foremost task» of a *Zoological Philosophy,* as quite distinct from improving upon Linnaeus' «magnificent construction». To the former end he relied on organs and organ systems by ranking them according to their general utility and to their modes of utilization by «higher» forms. However Lamarck did not go far in his main task; rather he kept having excruciating doubts on the actual rankings of organs and systems (cf. e. g. Vachon *et al.*, 1972: 258-263). Darwin entered evolutionary systematics by posing the problem of relationships in the far more ambitious terms of «real parentage» among species much as in a family tree — i. e. ideally in terms of a concrete measure such as generations. For him too this goal would be quite distinct from more practical purposes such as identification, to be achieved by diverse means (cf. his correspondence with Waterhouse, recently pubblished in full). Both Lamarck and Darwin presented their phyletic reconstructions through trees, Darwin's best known ones (in *Origin,* its only illustration) being very bushy. Having three to six branches at most nodes well fits a minor novelty that persists in its original habitat and also spreads in neighboring ones, any habitat tending to have two to five «neighbors» much as for borders among states. Be as it may, in Darwin's favourite dictum by Milne Edwards his bushy branchings refer to «variety» in which nature is «prodigal», while Lamarck's rare bifurcations obviously refer to innovations in which nature is «niggard».

As alluded in § 3 c), Darwin had laboured at great length on the phylogeny of barnacles, apparently through much the same principles as Lamarck's. Most likely due to this experience, in *Origin* (standard, Ch. XIV) he hended up concluding that «*analogical or adaptive characters, although of the utmost importance to the welfare of the being, are almost valueless to the systematist*» (analogical roughly corresponds to parallel). Instead «*very trifling characters*» would be the best indicators of real parentage if enough of them had been available, as hardly the case at that time (cf. later on).

Darwin's stand on systematics was soon reinforced as it started being realized how often similar or near-

ly identical animals had distinct origins, more often than not through «parallel» changes. Newmayr's first precise documentation of such changes stimulated Schiaparelli's «topological» approach in terms of switches among discrete, stable «fixed types» — i. e. resulting in a *tempo* akin to «punctuated equilibria» in contemporary jargon. Even if more efficient than standard character analysis, according to Schiaparelli his topopogical approach to whole animal geometry could not go very far in ascertaining the real parentages among animals. When his approach could actually be implemented, as was obviously far beyond the analytical machinery then available, Schiaparelli did not believe it would allow to sort out the relationships among animal phyla (at variance from his «mentor» Vignoli he believed they all had a common multicellular ancestor, c.f. Scudo 1991).

Established schools of systematics somehow managed to downplay, or altogether ignore the basic problems so clearly stated by Lamarck, Darwin, Newmayr, Schiaparelli, etc., as well as the rather different ones symbiosis was posing (cf. below). These problems kept re-surfacing, as for Hickling and Wenz uncovering far more telling examples than Newmayr's of distinct origins of «identical» animals — i. e. the evolutionary series of *Planorbis multiformis* in the miocenic, lacustrine deposits of Stenhaim, where three diverse modes of shell coiling can all appear, in a definite order, in the same individual (cf. e. g. Moret, 1940: 384). Shortly after, Piaget (cf. e. g. 1974) provided a deep behavioural and genotypical analysis of analogous shell changes in a living counterpart, *Limnaea stagnalis.*

Even ambitious theoretical analyses were often carried on nearly independently of prior theories, or of contemporary practice, or of both. Thus D'Arcy Thompson rediscoveder from scratich a «topology» nearly identical to Schiaparelli's, though more explicitly relying on organismal mechanics and subsuming continuity in evolutionary changes. An equally eye-catching difference is that Schiaparelli kept stressing his direct debt to Darwin, while D'Arcy Thompson kept elaborating on minor criticisms of Darwin (cf. Scudo 1991, Bouligand, these proceedings). Nearly simultaneously and independently of Schiaparelli, Rosa (1899) had proposed a theory that was also based on the limited morpho-functional variability within taxa, interpreting extinctions as mainly due to a great reduction, or exhaustion of this variability in the course of evolution. Interestingly, Rosa reasoned on morphogenetic processes and their changes in terms of reactions of whole genomes (ideoplasms) to conditions of life, firmly rejecting the approach in terms of ideoplasmic determinants and their struggles as by Weismann & Co.. He thus preceeded by decades Speeman's empirical characterization of induction as well as Schmalhausen's theoretical reasoning to be mentioned later on. Subsequently Rosa modified his theory in various ways, notably assuming that branching is always dichotomic; through Hennig this assumption eventually became very popular among practicing systematists, on all kinds of materials and with diverse meanings (cf. e. g. Baroni-Urbani 1977).

Meanwhile palaeontology was ever more firmly establishing a number of generalizations as empirical laws, such that the «pedunculum» of large taxa cannot be preserved in the record. In fact a major, very succesful change would have a small diffusion and a short persistance as such — most unlikely to appear in the fossil record — by soon giving rise to a major radiation. According to another major «statistical» law the most ancestral forms of large taxa tend to be «synthetic» and «polymorphic», in so far as the previous law allows to ascertain it (cf. e. g. Leonardi 1950). «Synthetic» means that the earliest *lineages* present diverse characters, each found alone, far more developed among late descendants. «Polymorphic» — i. e. «polytypic» in most posterior usages — means that in such early lineages individuals tend to differ for the presence or absence of one or more characters.

Symbiosis continued being widely regarded as a major mechanism in evolution mostly on the basis of general theories such as Giglio-Tos' (cf. § 1 c), though a precise knowledge was still largely confined to algal symbioses for animals and fungal ones for plants. A major advance consisted in Pierantoni and Sulk independently discovering, both in 1910, that the cells of previously enigmatic invertebrate tissues (pseudovitellus) are densely packed with fungal or bacterial symbiotes. The explosive increase in factual knowledge following this discovery made clear that all kinds of endocellular symbioses are common among protists while among metazoans algal symbioses are mostly confined to their «lowest» representatives, fungal endocellular symbioses do somewhat better higher uo in the «animal ladder» and bacterial ones still higher, up to colonial thaliaceans (where only taking place through most anomalous modes of development, cf. e. g. Pierantoni, 1940, Buchner 1965). According to Pierantoni this distribution would strongly support the symbiotic origins of eukaryotic organelles, a stand categorically rejected by Buchner who survived Pierantoni and had a far wider audience. As a result, the symbiotic origins of organelles was standard textbook knowledge in Italy around mid century, but it took decades before it was seriously considered again by the biological community at large (cf. Khakhina 1979 for analogous proposals by Russsian botanists).

Around mid-century Schmalhausen (e. g. 1946) was arriwing at conclusions parallel to the paleontological ones above mostly from embryological and biogeographical data, which he summarized into a single law of evolution of morphogenetic reactions (much as in Rosa's sense, cf. above). Briefly told, any novel reaction to conditions of life would originally be somehow proportional to the incidence and intensity of some external stimulus. If sufficiently persisting in a lineage, such a reaction would tend to evolve into discrete morphs, as threshold responses to external stimuli. Then each morph would tend to become fixed in a distinct lineage, so that individual conditions of life would only determine whether or not the «normal» development of the lineage can take place. The development of this single norm will then tend to become more and more «internalized» — i. e. selectively modified to mature earlier in ontogeny, regardless of conditions. The earlier in ontogeny its development is completed, the more a norm can be diversely modified later in ontogeny, mainly by the active reactions of individuals to different external conditions (i. e. it becomes «regulatory», cf.

also Scudo 1988, Wake, these proceedings). Taking into account that a single morphogenetic reaction often affects a number of characters, this law agrees with the palaeontological ones above as well as one could hope. It also accounts for different modes of interspecific associations being «statistically» related to basic development modalities — e. g. the «mosaic» development of metazoans, which mostly results in fixed norms of reaction, being more common in forms with strict biocoenotic ties.

The same law can also be directly recasted to specifically account for the evolution of symbioses. At first the individuals of a lineage either associate with a given «guest» or they do not — possibly associating with a somewhat different one — depending on conditions. The «host» lineage then tends to break up into one in which a given symbiosis becomes obligatory and another in which it does not take place — or another does — and this is often enough to prevent their intercrossing. Further evolution often results in the host «internalizing» key functions of the symbiote, then discarded. This last process is particularly evident, just by inspection, in several examples of animal luminescence such as the teleostean *Apagon* — i. e. the light organs of some species are powered by dense populations of bacteria while closely related species have nearly identical organs with endogenous light, and the intensity of its production is controllable at will. Being already evident that viruses can carry genetic information back and forth the cytoplasm and the nucleus (e. g. Teissier 1952), such transfers were no longer problematic.

At mid-century preexisting theoretical and methodological differences turned «virulent» through politico-ideological associations. Out of fierce battles a «new synthesis» emerged as the hardly contested winner, imposing a strict order in which earlier notions were rejected or «corrected» beyond recognition, while whole fields of investigation became «prohibited». Thus the tight forms of symbiosis emphasized in this review would not have been worthy of serious consideration, apparently by requiring the steady operation of «group selection» to get established (e. g. Williams 1966: 247), and by far too often eventually resulting in «inheritance of acquired characters». These are just two among a number of prior errors, such as «beanbag genetics» or «typology», that were codified mainly by Mayr (e. g. 1982), and to which I am unable to assign a precise meaning (Scudo 1993b).

One can easily follow, however, how the condemnations above went hand in hand with the spread of novel social usages, such as applying the term symbiosis mostly to bacterial and viral pathologies or regarding much, or most DNA of the higher metakaryotes as «junk» — i. e. a hardly controllable parasite. Synthetic theorists thus concentrated their attention on the severe conflicts that ought to arise between endogenous nuclear components and allogenous, or cytoplasmic ones, up to justify sex as a mechanism reducing or eliminating such conflicts (e. g. Hurst and Hamilton, 1992). To students of symbiosis in the old sense the same data pointed, instead, to viruses becoming the «preferred» endosymbiotes, through direct incorporation of their genomes, higher up the «animal ladder».

Another example of irreducible contrast between «the synthesis» and other theories comes from DNA coding regions having incurred in far more gene substitutions than individual selection could possibly account for. This was called «non-Darwinian» evolution and utilized to ascertain the real parentage among organisms much as Darwin had prescibed, mostly through a «neutral theory of molecular evolution». This theory would justify most changes in coding regions though random losses of alleles within finite populations, at a rate per generation that would almost solely depend on rates of mutation and thus provide a near ideal «clock». This theory overlooks that the changes it predicts could only occur if all individuals of local populations were shuffled at random at each generation, and much the same would also occur in whole lineages (cf. e. g. Karlin, 1969: 155 in particular, Nagylaki 1992 and Scudo 1992c). In fact, unless it were so, a genotypic variant could be lost by a whole lineage only if lost *at the same time* at all places were it occurs, and this has a vanishing probability. The «neutral theory» thus defies simple logics as well as the evidence that rates of synonimic base changes tend to be much the same, in long term averages, in organisms having as different generation spans as, say, elephants and bacteria. Only in this way synthetic theorists could avoid the basic error of «group selection» in darwinian theories starting from Wallace, according to which most hereditary changes would result from selection within populations and among them, unless reflecting past catastrophic events that wiped out most of the local populations of a lineage (e. g. Wright 1970, cf. also Scudo 1990).

In the light of the scatter of points just made major progress in systematics cannot be expected to mainly spring from more direct empirical evidence, no matter how useful any such piece of evidence could potentially be. Unless appropriately interpreted any direct evidence is likely to be soon forgotten, as it happened over and over again in the past. Being far from clear how to best utilize data of potential systematic interest, *all* promising leads should be pursued as far as possible. No matter how powerful on special features or problems *any one* systematic procedure now available could be, *on its own* it cannot go far in sorting out the real parentage among living beings. Major progresses in interpreting systematic data should hopefully come from Schiaparelli-like procedures, if nothing else since these have been among the least utilized so far (cf. Thom's, Bouligand's and Presnov's contributions). Also promising and hardly exploited is the fact that, early enough in development, changes in the dynamics of a single cell population can easily result in radical macroscopic changes (Giglio-Tos, 1900-1910, Vol. II in particular) — e. g. between bilateral and radiate symmetry, making one wonder about the possible phyletic meaning of «taxa» such as Radiata and Bilateria. To doubt the potential utility of topological methodologies in systematics since it has not yet been proven is the very last thing one should do. Only since a few years, for instance, Darwin's original guess on «trifling characters» for human populations is firmly standing up to evidence — i. e. their parentages as inferred by trifling changes in gene frequencies remarkably agree, among other things, with the phylogenies of their languages (Cavalli-Sforza *et al.* 1994).

Appendix - Gender systems and evolution

Here I shall explore the possible connections between the generalization on the roles of gender stated at the opening of § 2 c) and the truism that the metazoans and several metaphytes are characterized by lacking a gametic or haplont segregational gender system. Readers are assumed to be aware of the necessary botanical jargon and other technicalities.

«Loss» of the haploid gender segregation commonly results in monoecism among the otherwise dioecious Bryophytes in some of which, such as *Bryum* species, it is obtained by chromosomal duplication through apospory. The protandric gametophytes thus resulting are always infertile at first but they become sexually fertile, as in nature, after several generations of vegetative reproduction (von Wettstein and Straub 1942). In such cases the change from dioecism to monoecism must then be a semiautomatic one, quite likely bringing together both components of segregating, gender constitutive differences in the same chromosome complement. These would be arranged so that either of the two sets of genes for gametic gender could be turned on where and when appropriate, under the control of some «maternal» or «epigenetic» mechanism. Much the same kind of homogenization ought to also justify the sexual conditions of lycopods, whose prothalli can be strictly monoecious, or partially dioecious under genotypic-environmental control, or strictly dioecious in closely related species. On the other hand no trace of segregational mechanisms for haploid gender is evident among ferns as the homosporous ones are always monoecious, the heterosporous dioecious. Most likely, then, heterospory originated in ferns by homogenizing the haplont segregational mechanism after having reached a sporal dimorphism substantial enough to «preserve» haploid gender (heterangy, Thomson 1927, cf. again Scudo 1973).

The relationship between amphimixis, genomic sexual specializations and developmental complexity are only part evident, displaying the basic differences between haplont and diplont gender systems that Giglio-Tos had already recognized largely through *a priori* reasoning (cf. Scudo 1994). Haplont genomic dimorphisms always consist of constitutive diallelic gender differences and, perhaps, also of some reversible, epigenetic gender marking. When such a dimorphism becomes «strong» enough the segregational, haploid sex mechanism can be homogenized, thus resulting in monoecism as in some bryophytes etc. (cf. above). A still larger genomic gender dimorphism quite likely *forces* analogous homogenizations, such as those in the higher metaphytes and the metazoans (cf. also § 3 b). Among them, individual, diplont gender differentiations seem always to imply at least some degree of genomic, constitutive gender differences and some form of reversible, epigenetic gender marking proper, or other «clock» mechanism (cf. above). Some individual gender differentiation is *a priori* expected to arise in originally undifferentiated diploid systems as developmental complexity increases, and this could only be achieved by higher levels of genomic gender dimorphism that, beyond some point, can hardly coexist in the same individual whence diploid gender.

The tentative relationships between genomic gender dimorphism and developmental complexity inferred above necessarily take somewhat different forms according to whether development is an individual property, rather than a property of alternating generations or of some cycle of generations. It is evident, for instance, that amphimixis can be easily lost to hermaphroditism, hybridogenesis, pseudogamy etc. if it is just one stage in population cycles of developmentally stereotyped animals, such as wheelworms or aphids. This is hardly surprising since, in appropriate conditions, the repetition of a sufficiently standardized, long established developmental process could be achieved by sexual markings other than epigenetic. On the other hand it seems that more complex or less stereotyped animals can only loose amphimixis through exceptional changes such as interspecific hybridizations, or that amphimixis cannot at all be lost in natural conditions by the most complex matazoans and the higher metaphytes.

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POSTSCRIPT

Since this paper was written other works with analogous concerns were published, such as Margulis & Cohen's in Early life on earth (Columbia UP, New York, 1994: 327-333). Many novel molecular data are suggestive of special mechanisms in genomic integration that are still poorly understood — e. g. the removal of 28 uridines and the addition of 447 new ones in the ATPase subunit 6 precursor messenger of *Tripanosoma brucei*'s mitochondrion (Scott & Stuart, Science: 286: 114-117, 1994). Nucleotide linguistics is becoming a powerful tool to address all sorts of problems involving exogenous origins and genomic integration, such as identifying as «imported» a number of open reading frames in *Saccharomices cervisiae*'s mithocondrion (Pietrowsky & Trifonov, Gene, 122: 129-137, 1992). On the basis of many such novel data multiple origins of mitochondria look ever more likely. Also of great interest was to realize that the large intestinal symbiont *Epulopiscium fishelsoni* and related forms have Gram positive features (Angert et al., Nature, 362: 239-241, 1993) and lack a properly eukaryotic nuclear organization (e. g. Ahern, ASM news, 59: 519-521, 1993, their «nuclei» rather rensemble Gram positive endospores). These oximorons much strenghten the view (cf. § 3 b) that proper nuclear structures had late, quite likely multiple symbiotic origins. In this light *bona fide* chimaeras apparently between two eukaryotes in terms of rRNA sequences (e. g. Cryptomonas, Douglas *et al.*, Nature, 350: 148-151, 1991) would be more easily understandable if having in fact involved one a-nucleated partner.

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Systematics: is an historical perspective useful to understand modern debates on systematics and are we really equipped for sound evolutionary systematics?

Abstract – Consideration of the very early history of concepts in biology and of their influence on formal taxonomy shows that some basic current concepts are still rooted in extremely ancient ideas. Awareness, for instance, of the neoplatonic roots of modern trends in systematics, may be useful in the current debates.

That the last twenty or thirty years of debate over systematics have helped to revive interest in practical and theoretical systematics is obvious and this has, by itself, been beneficial. However I am worried that, unless the current arguments among the various schools are really clarified, we may run into as devastating a situation as it was with the neglect of systematics which plagued biology both prior to and immediately after World War II.

Anyone who has happened to read my papers on general problems of systematics knows that cladism, be it Hennigian or transformed, has been my special target over the last few years (Simonetta 1983, 1988, 1990, 1992, 1993). However I am not happy with *any* of the main schools of systematics. Indeed blind acceptance of this or that model of systematics by too many zoologists is swamping libraries with contributions which, should the particular creed of their authors be finally discredited, will fall to pieces, leaving heaps of sherds extremely difficult to handle and which will also not be easily disposable.

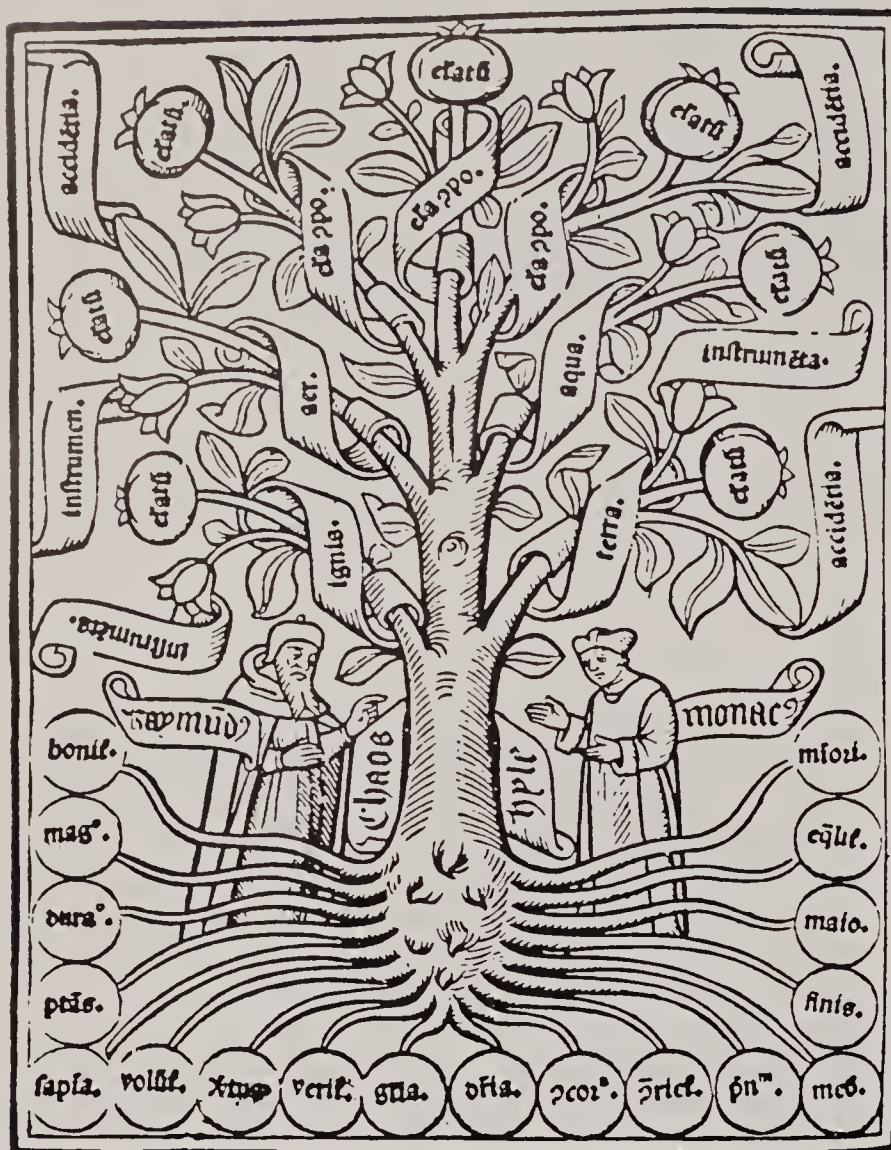
Here, both to avoid repetition of arguments which have not yet been challenged by disagreement, I shall suggest that there are other still poorly explored aspects in the systematic debate. I shall therefore outline some historical considerations, as I have a sort of feeling that the history of systematics, though it forms a minor chapter in any history of biology, had a subtle and underground role in shaping the groundwork of systematics which has been singularly overlooked.

In spite of repeated claims that systematics was born with Aristotle and that the arguments of ancient authors on the *scala naturae* are arguments about systematics, I think that, upon consideration, both claims misconstruct what Aristotle, Albertus and others had in mind. Although they did, indeed, provide some ready materials and ideas for true systematists, when finally evolved, they were really concerned with what we would call «comparative zoology» in a very broad sense.

Aristoteles' so-called classifications have to be pieced together from the Stagyrite's arguments, simply because probably he never thought to formalize then in a «system».

Aristotle was indeed the first and for over a thousand years, the greatest of zoologists, but he dealt with an extremely limited range of animals, and he could describe the structure, biology and some comparative morphology of some 500 kinds of animals without any need for a taxinomy. The very fact that in his writings the Stagyrite completely ignores a large number of animals which were both common and conspicuous in he regions where he lived for years, shows that he actually picked up for discussion those animals which, for whatever reasons, he deemed useful in order to elucidate some problems that he considered as being particularly significant. In some sense, just as the *Organon* was considered by Aristotle as an instrument for ascertaining the logical truth of statements, so his zoological books are aimed to point out significant problems of biology and illustrate by which methods and principles they could be clarified.

The wealth of zoological information built up very slowly until the end of the XV century, slower, indeed than that on plants, and for good reason. Herbals were first to be generally illustrated: illuminated herbals of Byzantine and Longobard times are still extant (the *Dioscorides Longobardorum,* copied in N Italy in the VIII century, the Byzantine codices of Naples, of the early VII century, and of Vienna, dated c. 512 A.D. and based for the figures on the illustrations by Cràteva, who was active in the early I century b.C.) and it is clear that they follow a pattern established early in the Roman imperial times. Indeed the problem of how to organize information became obvious to herbalists first, because physicians and apothecaries needed to identify plants correctly, if they were to avoid the risk of pisoning, instead of healing, their customers. Thus, since Theophrastus, plants were very often grouped, even if such groups were based on rather inconsistent criteria. For example in the catalogue of a (planned?) botanical garden in Mantova, the duke's physician G. F. Palperia, a contemporary of Aldrovandi, in 1625 had groups such as «*Plantae leguminaceae et trifoleae, Plantae tuberosae et carnoseae radicum, Plantae catarticae vel solutivae!*» (Franchini & al., 1979).

In the meantime Lullus (c. 1235-1315) and his followers built general theories of nature and knowledge on Scotist lines (cpr. Yates, 1982). They argued that during creation all the various qualities and powers of God imposed their effects on undifferen-

Arbor elementalis. Arbor vegetalis.

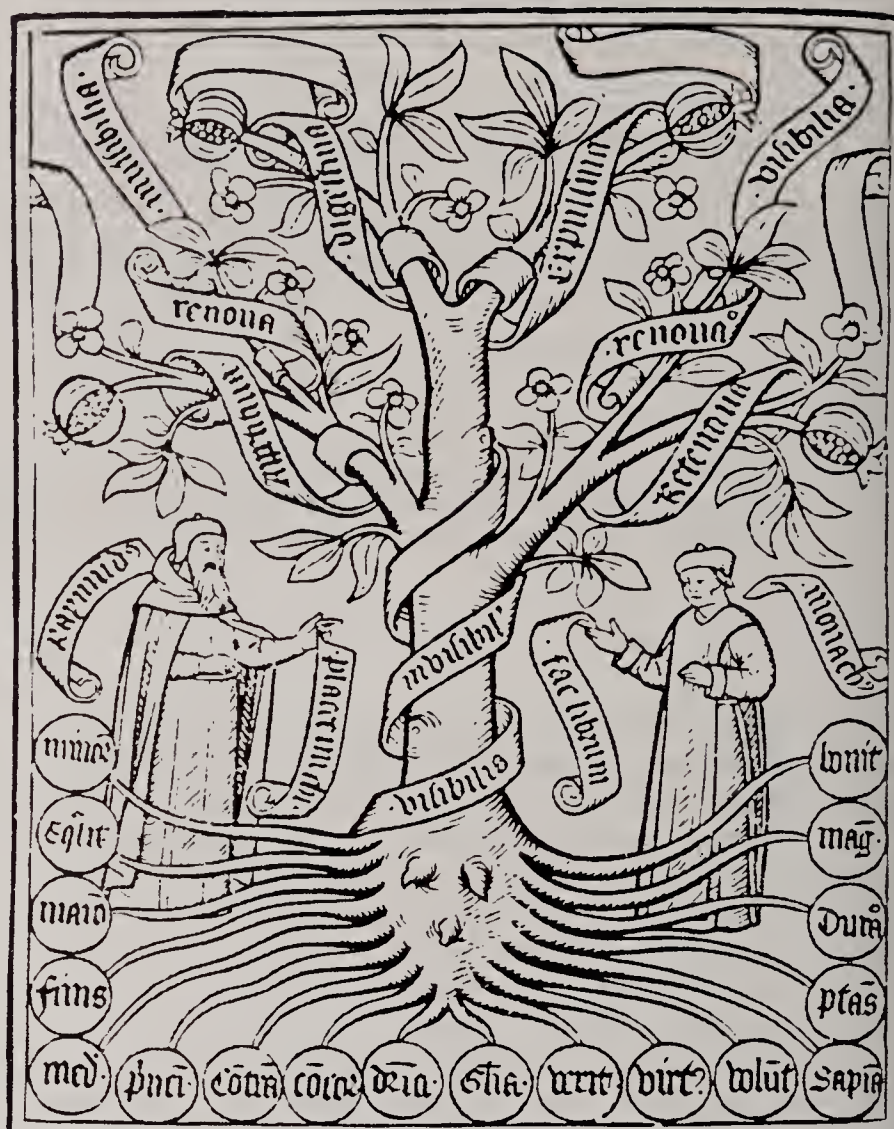



Fig. 1 - Examples of Lullist trees from a late XIV century codex, note the roots nourishing the tree and the leaves and fruits representing the world's realities.

tiated matter in various balances and combinations, basically through a double mechanism. First divine qualities impinged on the process of creation, and in Lullist Trees (Fig. 1) this is likened to the roots of the tree, by which it receives nourishment; second, by being variously redistributed by a hierarchy of progressively subordinated entities, be they angels, celestial bodies etc., the actual individual objects, the leaves, were at last created. And just as leaves are continuously shed and renovated, so it is with the turnover of creatures. As God was supreme reason, so creation must be, above anything else, logical, and by an appropriate logical instrument (in Lullism «combinatorial» logic) it can be penetrated.

At the same time the trees of creation, which could be imagined for all sorts of things, from animals to medical products and even intellectual entities, had to be reconstructed in their logical development and, as plainly stated by Dante «Ché non fa scienza senza lo ritenere avere inteso», this understanding had to be memorized in order to be mastered. Here the *Ars memoriae* came on its own and Lullus himself was one of the great masters of it (cf. Yates, 1982, Rossi, 1983).

If one considers that, probably under the influence of Arab scholars, Aristotelean categories were considered as being real material operators in the framing of the world and so were such divine qualities as *Bonitas, Misericordia, Justitia* etc., one perceives that the debate between Realists and Nominalists, during the late medieval times was much more complex than it is usually described in texbooks.

At the eve of the XVth century the true aristotelians had moved well away from orthodox aristotelism into a nominalistic epistemology (properly named «terminism»), while naive realism had developed into Hermetic-neoplatonism and Lullian trees were familiar as expressing not genealogical kinship, but the equally true generation kinship.

Then the age of explorations and discoveries swamped the scholars with innumerable new kinds of animals and plants, and they were faced with the Herculean task of organizing this new knowledge. At the same time the rarity, oddness or sheer beauty of the manifold products of nature stimulated the natural tendency of men to collecting, and museums were born.

I have just said that at that time scholars were provided with two alternative intellectual tools for their task: traditional Aristotelism turned nominalistic by the medieval university scholars, or Neoplatonism-Hermeticism-Paracelsism, rooted in Lullism, with a strong realistic tinge and commonly credited with an Augustinian parentage, which made it, if not orthodox, at least defensible on religious grounds.

People like Aldrovandi and especially Cesalpino tried to use the first tool; others, for instance the groups linked with the Academia dei Lincei or the Royal Society (like Ray), the second one.

There is indeed a subtle difference between the ideal Museum of Aldrovandi (now preserved, to-

gether with all the accompanying notes, by the University of Bologna), which he conceives as a sort of material Encyclopedia, the precise counterpart of a set of files (and indeed he did file all the specimens of his own museum in the most complete and exaustive way, with all sorts of cross references etc.), a source of retrievable information, the more general and complete the best, and the Museum seen in the light of Lull's «Ars». This second kind of museum is a material itinerary symmetrical with the «World's theatres», a sort of treatise built on specimens, in which the relevant ideas are linked into an organic, chained argument, which will lead both to remembrance and to knowledge (cpr. Rossi, 1983).

Both kinds of musea are still with us: the lullian one in the public exibits, which tell one story, and Aldrovandi's in the study collections, where alternative stories are developed.

Books, being musea in words, had to follow or, perhaps, to be the blueprint for the material musea being assembled.

It should also be noted, as it is customary to assume that the «Baconian» scientific attitude superseded the medieval one and that modern science has broken with both the platonic and the aristotelic tradition, that Sir Francis Bacon himself largely departed from his own principles when writing of Natural History: His *Parasceve ad historiam naturalem et experimentalem* and other writings clearly expound principles which are directly linked with those of the *Ars memoriae*» (cpr. Rossi, 1957).

John Ray, whose great influence in framing the principles of systematics has always been aknowledged and who was especially influential on Linnaeus, is known to have developed his basic systematic principles while, collaborating with Willoughby and Bishop Wilkins for the development of the «universal language», Ray actually developed a special classification for Wilkins that was actually conceived as an integral part of the project and was strictly based on logical division, though he was quite unhappy with it as he thought the framework too rigid and of limited scope (cpr. Rossi, 1983, Mayr, 1982).

Thus, it seems conceivable that, more or less consciously, the joint requirements of a realistic-neoplatonic frame of mind, which was prevalent in Northern Europe, and the requirements of cataloguing specimens did naturally lead to the kind of classification which we call Linnean.

Linnaeus was an exemplarly practical mind and did not generally delve into purely theoretical speculations (when he did he occasionally made the grossest mistakes, such as when he denied the existance of spermatozoa as living beings). Linnaeus generally formulated his theoretical ideas in the form of brief statements and rather set himself to improve and generalize on paths tentatively trodden by others.

However there is no doubt, as it is amply borne by his repeated hymns to the Divinity, that he regards, true to the neoplatonic tradition, that the correct and «natural» listing and describing of being led to true knownedge of God Himself in his works, which is a classical attitude in Medieval theology of truth. Moreover, when we examine the various stages of the development of his classification of plants and his discussion of the theoretical principles on which he built his work, there is no question of the influence that the combinatorial mnemotechnics and the lullist tradition had on him: in fact he first derived his 26 basic characters which, also because of their number, he called *Litterae vegetabilium,* then by combinatorial methods he joined them into «words», which characterized his taxinomic order, and he had no doubt that the «empty» words would eventually be filled by new discoveries, which is pure Leibniz.

To discuss the various traditions, besides the neoplatonic (such as the Augustinian-Lutheran), which may have been at work in shaping Linnean systematics would need a book, rather than a paper, and thus I leave this point, simply recalling that Linnaeus' father and grandfather were Lutheran preachers.

For the whole of the XVIII century and the first half of the next biologists had to choose between two alternatives: either they subscribed to the thesis, honoured by all Christian creeds, that the natural world, being the work of God, portrayed the same orderly Supreme Mind and was built of logically and indeed necessarily related objects, shadowing a Lullian tree; or else they took a definitely atheistic view, as D'Holbach and several French did, but to the same practical result.

Indeed, by the XVIII century classical scholasticism had become entirely discredited in protestant areas and among «Libertines» everywhere. But also in the Catholic media, where, because of the authority of St. Thomas Aquinas, the bulk of scolastic phylosophy was still generally studied, it was customary, out of the classroom, to decry it. So, down with scholasticism went nominalism.

Anyway, ever since Aristoteles had used the word «genos» to band related items or concepts (and he was justified by Greco-Roman tradition, where the «Gens» was supposed to share the same «Genius» even when relationship was rather by religious traditional links than by real blood kinship), the term, which could have been translated indifferently either as «genus» or as «Family», was familiar in science and philosophy with this ambiguous association both to kinship by the mechanisms of creation and by real reproductive continuity.

Thus the framework for evolutionary ideas was prepared: Once *generatio aequivoca* had been generally discredited, living beings were naturally considered as being related, at least kind by kind, by genealogical relations which, just as human family trees, could be expressed by dedrograms, and the «little» step of limited evolution, such as advocated by Buffon and by Linnaeus himself in his later years, was self-suggested by the usage of words such as family and Genus, with their strong genealogical implications.

Indeed it seems that during the XVII and XVIII centuries and well into the XIX century, the majority of the best general zoologists and botanists were rather subconsciously dependent on Platonism (actually Goethe was a spinozist in philosophy, but rather a platonist in sciences and such Naturphilosophen as Schelling or Ocken were openly platonists), while the great comparative anatomists and pysiologists, such as G. Cuvier, were more «aristotelically» minded, with Darwin nicely in the middle, pragmatically taking the best of both.

Darwinian theory, turning biology to a large extent into a historical science, should have reopened the issues, as Aristoteles himself had noticed that histo-

rical statements could not be verified by classical logics, and the difficulty had been further exaustively analyzed by medieval scholars, who had shown that any proposition where time was involved can not be proven by dichotomous logics.

However, Darwin himself and most of his followers, including those who plunged into an all out attack on traditional religions, generally avoided the more theoretical implications of their stand and may even have been unconscious of pressing into their services time honoured devices, which had been originated for quite different purposes, as one may see, for instance by comparing the «trees» of the pious Lullus (Fig. 1) with those of the atheist Haeckel (Fig. 2): they were too busy establishing the fact of evolution and its mechanisms, to worry about its implications for systematics. More specially, though at least Darwin himself was aware of it, they should have given more attention to the impossibility to reconcile the endeavour to reconstruct a historical narrative of which the individual specimens known were episodes (just as artifact or documents are in human history), with a belief of the reality of taxa, which was rooted on entirely different principles; and that while «Linnean» taxinomy, as it was practically the best possible in order to manage the evidence, had to be preserved and used.

As I have argued other aspects of the debate on systematics elsewhere, I shall not repeat here my arguments in favour of regarding formal taxinomy as a necessary, albeit, conventional tool for all biological researches (Simonetta 1992, 1993), rather I have been aiming here to show that, as we are human beings, we are, willy nilly, the products of cultural evolution, is it possible that in the minds of each one of us the ghosts — the old archetypes — are still living and moulding our approach to systematics?

For instance, I feel that there is a case for arguing that the practice of certain algorithms in cladistic, and especially transformed cladistic systematics is «phylogenetically» related with some Hermetic-cabbalistic renaissance practices, through Oken (with his dichotomus differentiation, advocated in his «*Lehrbuch der Naturphilosophie* in 1809 and his slightly previous, proclaimed «neopythagoric» phase), Gothe, Franz Baader and others.

Consideration of the medieval «terministic» debate recently led me to consider the study of the messages relayed by the scientific literature and whether its semiotics should not be propedeutic to consideration of the philosophy of biology. Though I have not gone far enough to have any definite ideas, I have a strong feeling that consideration of what really happens in the sequence: «observation of evi-

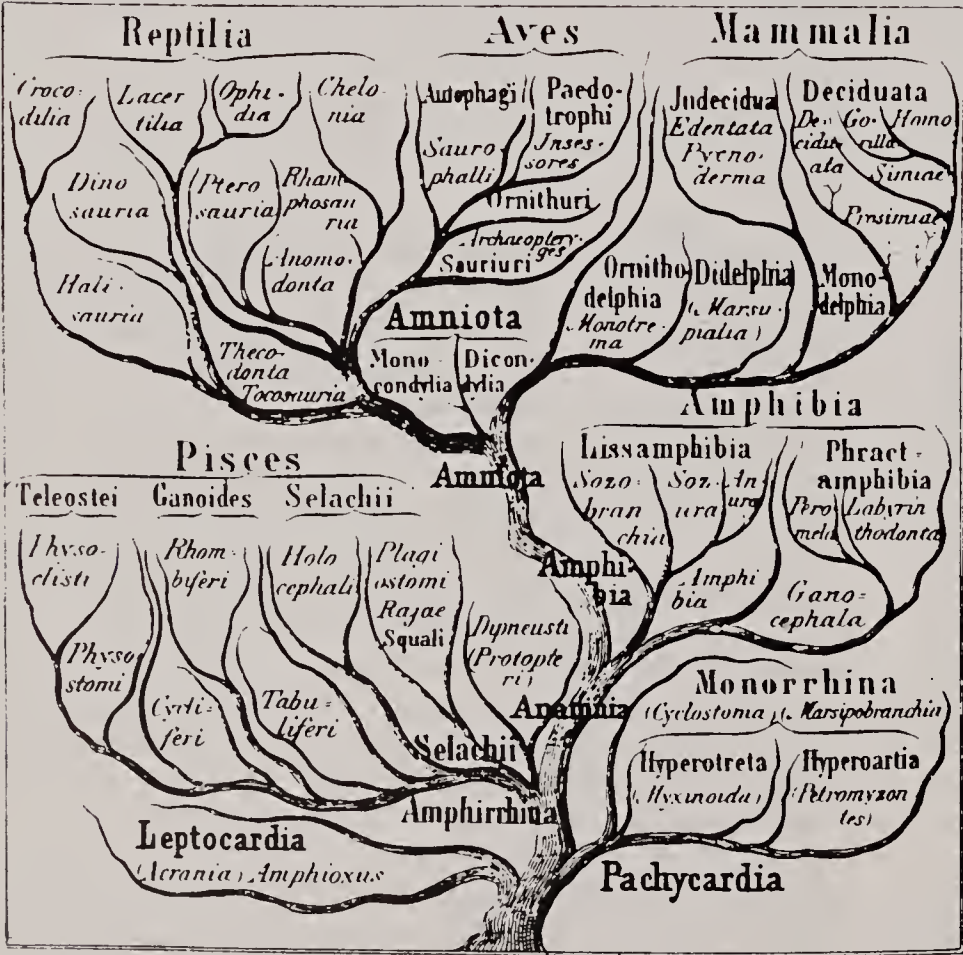



Fig. 2 - Two of the many «trees» proposed by Haeckel, leaves and fruits are substituted by names, but the similarities with Lull's imageing is obvious.

dence→ organisation and interpretation of it→ transfer into verbal information→ interpretation of verbal information», may really contribute to our debates. Indeed, when we consider this sequence, it is clear that we have here a process of progressive abstraction and that the result is only related to the phenomenon, but that the relation is an indirect one. It appears that modern semiotics (cf. Eco, 1990) largely revive the positions of medieval terminists maintaining that concepts and more generally all collective terms «stand for» something, are *suppositi* for something real, but that they imply a «presumption» about them, which implies a complex attitude to knowledge: strictly objective knowledge being absolutely denied, while a probabilistic, if necessarily biased, knowledge being both possible and valuable.

Subjective bias in presumed objective methods may more or less always be proved. For instance it is easy to show that all kinds of cladistic analysis are based on strictly typological assumptions, which are and work independently from the proclaimed evolutionary and systematic principles of the same authors who perform them.

It is a well known fact that, while any writer, including the scientist, puts himself into his work, his work while being written, impinges on the writer subconscious and shapes it, just like any other writing he has happened to read since his childhood. Therefore it is not surprising that, in biology, such a long tradition of «realism» urges so many excellent scholars to strive for a «system» good for all seasons, for the «good» species concepts, for «rules» which will work out the relationships of living beings with regular reliability.

There is an almost general consensus that the «system» must mirror, as far as possible the best evolutionary reconstructions. However the real scope and the essential autonomy of phylogenetic studies with respect to systematics must be fully understood. Hennig (1966), as usually wrongly, maintains that phylogenetic connections are among species or among taxa of supraspecific level; obviously it is perfectly legitimate to study the relationships of abstract concepts, such as classes, but this is essentially different from studying phylogeny (See Simonetta 1992, 1993). Indeed phylogenetic studies are concerned with the possible relationships of known specimens, which are assumed to mirror the relationships of the populations past and present to which these individuals belong; formal systematics, instead, is a message with a complex function.

If we fail to make here a clear distinction between the reconstruction of phylogenetic connections and formal systematics, instead of having a «one way» lane from evidence to interpretation, and from interpretation to filing and retrieving both the information and the interpretation and stop there, we shall always be in danger of a feed-back: assumed systematics impinging on interpretation of data or, worse, a systematic arrangement built on some presumed rules prompting a stereotyped way of reading the evidence.

Should not we instead be afraid of all kinds of orthodoxies and endeavour to fight them?

Having thus tried to give a bit of attention to what may, perhaps, be deemed a marginal aspect of the debate, but one that I feel to be significant in the study of such an elusive problem as that of the significance of taxa, a big query follows.

Have we got a really good theory of evolution, improving consistently on Darwin's? I am afraid that we have not.

Granted the basic Darwinian principle of variation and selection, both stabilizing and directional, on one side none of the current general accounts of the theoretical aspects of evolution, does take into full account *all* known facts of genetics, nor do they account for *all* the different ways selection has been shown to operate both as individual and as group selection. We have no really satisfactory *general* explications for the coordinate evolution of complex morphological, physiological or ethological patterns, nor for the apparent fact that some kinds of mutations or some types of selection are prevalent among certain organisms, while alternative ones are commoner in other, sometimes related, groups. Finally we have several elegant and attractive models of evolutionary events, especially in morphology, where they stem from Schiaparelli's and D'Arcy Thompson's pioneer work, but we do not really know how to correlate them with known facts of genetics and of natural selection.

If we, as I expect, agree that systematics should mirror, as far as this is practically possible, the course of evolution a «new synthesis» is needed against which theories and practices of systematics must be tested, and I expect, found wanting.

In the meantime, I am afraid, we have to go on by old principle that a good taxon is that which is maintained by a good systematist.

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René Thom

Qualitative and quantitative in Evolutionary Theory with some thoughts on Aristotelian Biology

Abstract – This paper aims to show the relation between qualitative and quantitative considerations (in Biology and elsewhere). It is argued that quality cannot be reduced to quantity, as is so often held with conviction. We propose applications of qualitative thinking for the Darwinian problem of speciation and discuss Lyell's «uniformitarianism» applied to Darwinism. The discrete qualitative character of cellular morphogenesis necessarily entails *qualitative discontinuities*, however small these may be quantitatively.

It is now commonly held that any qualitative difference may be expressed quantitatively. The old saying of the British physicist Rutherford (around 1900), «Qualitative is nothing but poor quantitative», is a statement that most of today's scientists are quite willing to endorse. For obvious reasons, the computer science industry of this last half-century has done quite a lot to impose the idea on the public mind. But it may now be time to react against this widespread belief.

One may wonder why a former mathematician should find it necessary to defend the essential specificity of quality, a concept somewhat alien to the world of numbers. In the same way, one may wonder why biologists have been so eager to tread the path of quantization. Think, for instance, of the impact of the statistical school of the early 1900's (Fischer, S. Wright, after Galton...) which led to the triumphant revival of Darwinism under the name of neo-Darwinism. Classical biologists used, around 1800 when their science was new, the concept of *animal organization.* The Latins knew the locutions *Situs Partium,* the Greeks *sustèma tôn moriôn.* Now people believe that it's all in the DNA and that life is more interesting at the molecular level – inside the cell – than at the gross level of «big animals». Yet I hope that among my hearers a sufficient number will agree that the study of «large animals» is still a rather significant part of Biology.

Now, is animal organization a qualitative or a quantitative concept? The answer is not so easy. For quality frequently creeps into mathematics under the guise of number. Is the quantitative inequality $a < b$ (a less than b) a quantitative or a qualitative relation? Consider the integers 1 and 2. Most people would immediately say that the relation $2 > 1$ is a quantitative one, as $2 = 1 + 1$. But the couple of integers in the order (1, 2) is not the same as the dyad in reverse order (2,1): here enters the plane, the continuous 2-dimensional Euclidean space (endowed with horizontal and vertical gradients) needed to write down the formula. Because of this spatial embedding, the two dyads (1,2) and (2,1) have to be considered as *qualitatively* different. Our grammars justify this viewpoint by distinguishing the *cardinal* number (of nounlike function) from the *ordinal* number (an adjective). There is little doubt that the consideration of an organ's relative position with respect to others', fundamental in defining *homology* between similar bones or organs in different species (remember Owen's definition as quoted in Professor Minelli's paper), refers to this concept; and this also requires that a system of three «gradients» (or space coordinates) be specified. Another apparent intermingling of number and quality occurs in topology. Consider the topological classification of closed oriented surfaces. Such a surface can always be constructed by adding k handles to the standard two-dimensional sphere S^2. This positive integer k is called the *genus* of the surface (the cases $k = 0, 1, 2$ are realized respectively by the two-sphere S^2, the two-dimensional torus T^2, and the *Bretzelfläche).* Here the differences, although expressed by a varying integer q, the genus, are fundamentally of a topological, qualitative nature. Hence the answer: *Many apparently quantitative relations are in fact of a qualitative nature, inasmuch as they involve topological relations more specific than those of the quantitative ones.*

After all, between *situs partium* and *analysis situs,* the name given by Leibniz to topology, there is an obvious affinity. When discussing a numerical equality $a = b$ with regard to two entities A and B, one has to distinguish the case where a and b relate to observable characteristics of distinct entities A and B from the case where A and B are shown to be identical through this equality of measurement. For example, two quantities of the same matter and of the same weight are interchangeable. It is clear that if we consider two evaluations of identical quality in two different entities A and B, that does not imply the identity of the two «substances», in philosophical terms. Since $a = b$ is the most typical form of relation, it would be useful to analyse the medieval distinction between substance and predicate. To do this we place ourselves in the framework of Aristotelian metaphysics, which has brought to the study of this problem some intuition that is still highly relevant.

The relation of Genus to Species

The couple Genus-Species, which has not yet disappeared from our taxonomies, owes its definition to Aristotle. Needless to say, this definition is infini-

tely broader than the usual biological use of the terms. In Aristotle the notion has a logical origin. Two qualities (a) and (b) are said to belong to the same genus (Γενοσ in Greek), if, whatever the entity X, the two propositions: *X is a* and *X is b* cannot be simultaneously true. In other words (a) and (b) are *contrary* (a wider notion than *contradictory,* where the genus is in one dimension). This means that, in a metaphorical sense, qualities (a) and (b) compete with each other to occupy a space (G), which must be considered as a piece of matter in the sense of Aristotle's *hylè,* that is to say a continuum (*suneches*) similar in principle to the Euclidean one. In particular, one can by mental experiment *continuously deform* concept (a) into concept (b) (and vice versa) without ever, throughout this deformation, having the impression of any brutal discontinuity in the nature of the affect.

On the contrary an affect such as (a), endowed with a certain psychic individuality, will be called a species *(eidos)* of genus (G). In theory two species within the same genus can always be deformed one into the other in a continuous way (*). It can be argued that this notion, valid for man, is also to some extent present in the animal psyche. For man it is always possible to shift from one colour to another without quitting the space of colour measurement. But (unless one is under the influence of mescaline or some similar drug) one cannot transform a colour into a smell or into a tactile sensation. There are two basic genera: time, each instant of which is a species, and one-dimensional Euclidean space (where each point is a species).

If the relative autonomy of the nervous system governing perception is sufficient to explain the autonomy of the five senses, the same explanation is not available for abstract concepts, the adjectival qualities of our languages. But at least we may imagine a topology of adjectival concepts allowing them to be associated with a semantic distance, and by and large, this semantic distance verifies the inequality of the triangle

$$d(BC) < d(BA) + d(AC)$$

provided qualities A, B, C belong to the same genus.

Aristotle, in his Logics, laid down as a principle that if we have two genera, G1 and G2, either one of them is a sub-genus of the other (e.g. white man is a sub-genus of man), or they are «incommunicable»: *Ouk estin eis allo genos metabasis* (there is no way of passing from one genus to the other). This affirmation led Aristotle to accept that all science is reduced to the study of a genus, there is no universal science. But we may wonder whether the articulation of subgenera in a genus does not proceed from universal mechanisms. I, for one, believe that the model proposed by catastrophe theory (the cusp model) could be a good candidate, particularly for the transition genus — species, object of zoological taxonomy.

This problematics surrounding the incommunicability of genera plays an essential part in the question of the relation between quality and quantity, the subject of this essay.

Even if we accept the universality of the cusp model in the division of a genus into its species, there is nothing to show that the different potentials we have to consider between genera can be connected by a quantitative relation, of an algebraic nature for example. Belief in the possibility of expressing in a quantitative way relations between different genera has engendered semantic monsters in our everyday vocabulary. Take the paradigmatic example given by the *quality-price* ratio that serves in gastronomical guide-books to rate different restaurants — the direct, positive side evaluating the quality of the setting and cuisine, and the opposite, negative side, concerned with the price. But the idea of quantifying these effects by means of a quotient remains in the realm of mythology.

Now let's come back to Biology. There is around at the moment a much-used but ill-defined concept, that of *cellular type.* It is agreed, or so I read recently in a very serious journal, that there are about two hundred types of cell in the human body. But I have seen no table of these types and have no idea of their organizational modes. It was suggested to me that the mode of genome activation was an essential part of this definition. But I suppose that the old classical designations of tissue (epithelium, mesenchyma, free cells, etc.) continue to play a part in the new taxonomy. However that may be, we have to believe that this classification is of a «discrete», qualitative and finite nature. It seems to me that this must have some impact on an old evolutionary problem. Is there gradualism, or, on the contrary, catastrophism, attending the apparition of a given speciation? Darwin contented himself with Lyell's gradualism. Yet we can hardly deny that there have appeared, at certain times, very considerable innovations (a typical example is the apparition of the amniotic egg in amphibians). If we look at the graph constituted by cellular types in the course of ontogenesis, we see that new types *must* have come on the scene from time to time, even if, from a quantitative point of view, the clone so realized may have been very slight. Whence a *formally necessary* response: There have indeed been qualitative innovations, even if their immediate quantitative effects remained unobtrusive. Quantitative gradualism stands to reason, after all — one cannot imagine a mother giving birth to offspring larger than herself — but the apparition of a new mode of life made possible by qualitatively new types of cells can turn this innovation into a subsequently notable transformation in taxonomy.

In conclusion, I would like to draw attention to the unifying character of this definition of the couple Genus-Species. We shall call «affect» all modification of perceptive data in an individual that is of a clearly individuated nature. There exists then a relation of equivalence between affects of subjective origin, which makes it possible to recognize whether two affects are of the same type (for example, phenomenological equivalence at two points in the exter-

(*) Some genera, in Aristotle's sense of the word, obviously have a discontinuous matter. Take the descendancy of a single human ancestor, example given by Aristotle for the entry Genos in his book Μετ Δ 28. In this case we have to consider that the *matter of the genus* is engendered by the generative dynamics represented by relations of filiation making a connected space of the human group.

nal medium observed). This last relation of equivalence leads one, in the case of the observation of living animals or dissected cadavers, to a classification of equivalent parts by their aspect, Aristotle's *homeomerous parts.* We are led to an objective definition of biological organization: the stratification of the organism into homeomerous parts. In a *semi-algebraic* model, as suggested by Schiaparelli, this allows us to recover the homotopic diagrams of d'Arcy Thompson and consequently to define Owen's homology in a conceptually rigorous way. The decomposition of a concept into genera and sub- genera becomes an operation (application to the data of a local relation of phenomenological equivalence, or in algebraic terms, a relation of equisingularity) similar in nature to the decomposition of an animal organism into its «homeomerous» parts. In the case of a concept, we have to classify its extension by identifying its prototypical elements, centrally placed, and throwing aberrant elements out toward the periphery. *Categories* are universal genera through which such an analysis may be carried out.

Having defined, in his study of living bodies, the notion of *homeomerous parts* characterized by the property of local phenomenological equivalence between two points of the same stratum, Aristotle felt it necessary to introduce also those parts which already have specific names in our ordinary languages, the usual body parts — in the case of human beings: head, neck, chest, belly, legs, arms and so on. Such parts are usually formed by the aggregation of several (at least two) homeomerous parts, conveniently limited. He called them *anhomeomerous parts*, the seats of active functions and operations (erga kai praxeis). If homeomerous parts can be described by a stratification of semi-algebraic nature, these new kinds of parts cannot be split up in the same way. Their breakdown fragments the homeomerous strata. Take for instance the inclusion thumb $\subset$ hand. The boundary between thumb $\cap$ hand-minus-thumb is realized in bony tissue by a well-defined smooth surface, the phalanx-metacarpus joint. The same is no longer true for any homeomerous part of the surrounding tissue (flesh, nerves, tendons, etc.). And the blood, contained in the vascular system, is not properly a homeomerous part because its ramifying boundary shows signs of fractality (*Partibus Animalium* 565b 21-22). The observation that any functionally active (anhomeomerous) part of the human body contains at least two kinds of tissues is one of the Philosopher's most penetrating insights.

See for instance my astide:

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Adam Urbanek

The origin and maintenance of diversity: a case study of Upper Silurian graptoloids

Abstract – Empirical studies on fossil material reveal certain features of the fossil record which are of great importance for the generation and maintenance of biological diversity. This is particularly clear in respect of the stem species (lineages). Their persistence in time, combined with an ability for iterative speciation, accounts for many important events responsible for recoveries and diversifications of the fauna. Stem lineages provide a reliable test for the conversation of evolutionary potential in spite of the numerous branching off of the lineage. This may be called a historical experiment, as it proves that deterministic factors, along with the contingent ones, played an important role in evolution.

In the real course of evolution, as seen in the fossil record, diversity is generated due to so-called adaptive radiation. As a rule, recovery and re-radiations start from indigeneous survivors from biotic crises. They are subject to a population explosion combined with an increase of variation, both being related to an ecological release. This variation is later used as raw material for speciation and transpecific evolution. The early phase of radiation is marked by the paucity of lineages, and the presence, along with generalized or synthetic types (species or species groups), also of specialized lines of evolution. The former produce long-lasting lineages and frequently are subject to secondary radiations, whilst the latter become extinct after some temporary success. In many groups of the Graptoloidea, being the dominating element of the macrozooplankton in the Early Palaeozoic seas, evolutionary changes are concentrated on apertures of zooidal tubes. This may reflect improvements of the feeeding apparatus and feeding mechanisms. Trophic specialization is a golden thread of the evolution in this group. Production of as many character differences as possible, within a certain basic adaptive type, enables the subdivision of the trophic niche and relaxation of competition between otherwise very similar species. Hence, advanced representatives of particular lineages were usually K-strategists, while the ancestral species bear more or less distinct traces of an r-strategy. Seen from a historical perspective the evolution of graptoloids looks as a process of diversity and trophic specialization increase, punctuated by biotic crises. After each biotic crisis the extermination of specialized types was followed by a re-radiation from non-specialized survivors.

Inductive phylogeny

A study of the history of fossil taxa and phylogenetic relations among them may be considered the core of any palaeontological programme. Studies in other fields of palaeontology are, in one way or another, related to this basic research programme – in other words they are derivatives of the historical and phylogenetic approaches.

Dealing directly with remains of organisms of the past one can trace morphological changes in the succeeding fossil populations from subsequent horizons. A comparative anatomical analysis, combined with morphometric (biometric) methods, makes it possible to measure certain parameters of evolutionary change and to trace the variation range, mean value, and standard deviation, as well as to apply more sophisticated methods (like multivariate analysis etc.). Essentially qualitative morphologies could be transformed in this way into largely quantitative data sets, which could later serve for discrimination of species and other taxa. Such data, combined with radiometric age, may be instrumental in the evaluation of certain parameters of the evolutionary process which are not directly observable.

Studying fossil organisms enables the application of inductive methods to phylogeny, when phylogenetic inferences are based largely on empirical data, namely on the observed direction of changes and succession of chronodemes (fossil local populations) in time. This introduction of the time factor and an essential parallelism between morphological change and time, limits considerably the degree of subjective and speculative elements involved in phylogenetic inferences. The application of an inductive approach also increases the probability of phylogenetic inferences, and in the case of densely-sampled, numerically abundant and biometrically analysed populations composed of well preserved remains – they approach certaintly. Such highly reliable phylogenies constructed with the use of the inductive method were described among others also in graptolites. (e.g. Urbanek, 1963, 1966, 1970; see also Bulman 1971).

I apply the term «inductive» to phylogeny merely to stress the importance of inferring generalized conclusions (on ancestry or relationship) from partial facts concerning fossils, from the changes observed and their succession in time. I would rely on the real course of events, established in the above way, rather than on considerations based on similarity and its evaluation (homology). By using the term «inductive» I would also like to emphasize the significance of bringing together and adducing disparate facts making up the real history of fossils.

The research programme as advanced above cannot be applied in every case – too frequently the incompletness of the record makes the use of the inductive approach impossible. However, the inductive programme should be realized whenever possible. It brings most interesting results, some of which I am going to discuss below.

Considerations that will follow are based on the study of a single fossil group – the graptolites. They were colonial, marine hemichordates of the Paleozoic Era, related to Recent pterobranchs (represented e.g. by *Rhabdopleura*). Some were benthic and sessile, but we will focus on «true graptolites», of the
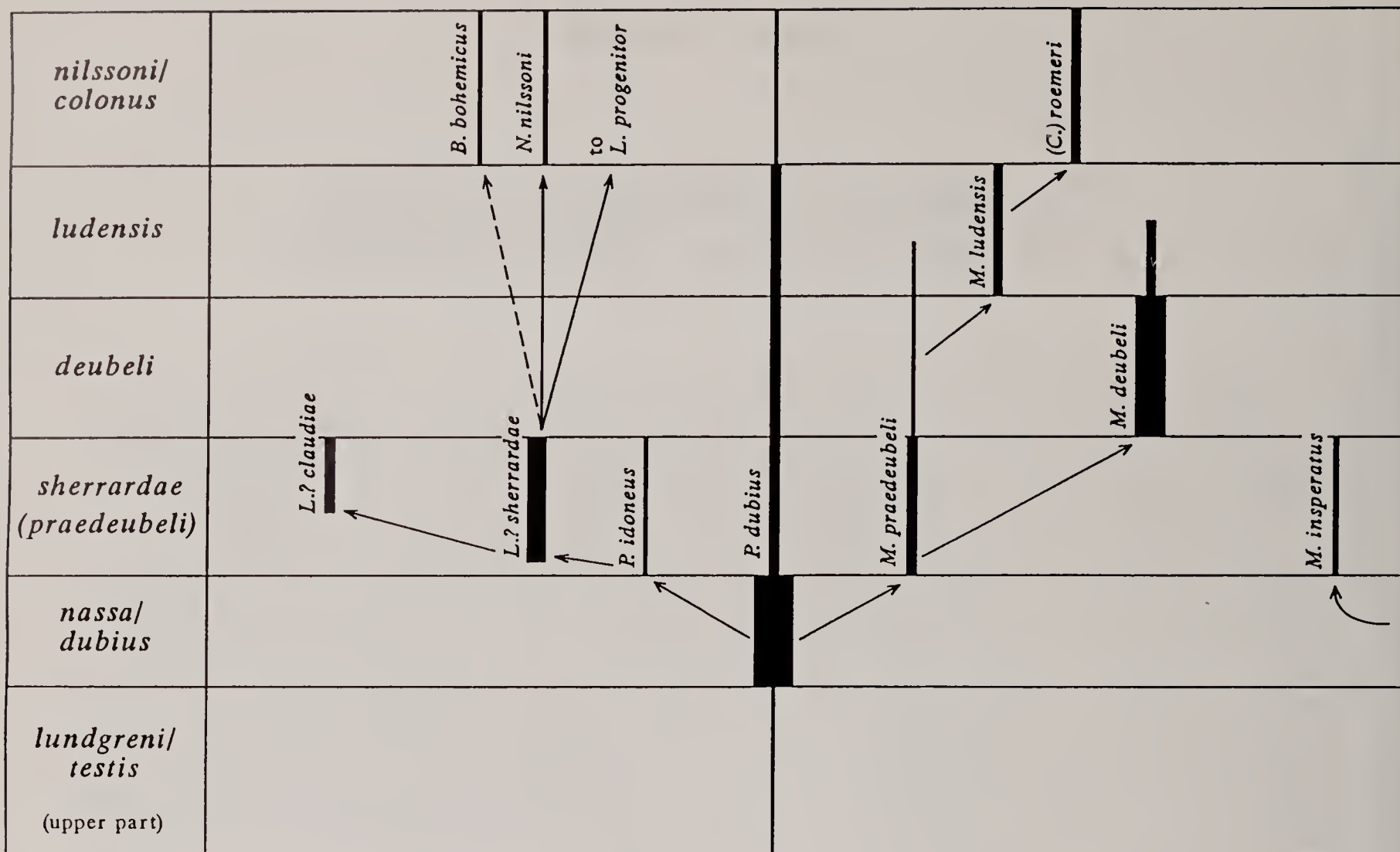
Fig. 1 - Early phase of monograptid radiation after the *lundgreni* Event. Note the population burst of the only survivor, *Pristiograptus dubius* (Suess) as indicated by a thick line, and its early schism into two main lineages. An important role was played by *Lobograptus? sherrardae* as a generalized or synthetic species (from Koren' & Urbanek).

order Graptoloidea. They were planktonic and in most cases pelagic. The specialized Silurian monograptids had a simplified organization, and their colonies were composed of a series of zooids budding successively from each other and capable of secreting individual lodgings made of sclerotized collagenous fibrils and called thecae (see Fig. 4, th_2). The overall morphology of the skeleton of the colony (the rhabdosome), as well as the structural details of the thecae serve as the basis for distinguishing a number of genera and species. Displaying usually a rapid evolution and frequently a world-wide distribution, the graptoloids («true graptolites») supply a number of interesting instances of evolutionary change.

The problem of stem species and the nature of historical experiments

One of the most interesting taxa revealed by the study of phylogeny on fossil material are *stem species*. They may be operationally defined as persistent and conservative lineages producing, by means of iterative speciation, some daughter species, but otherwise showing a predominance of stasis or near-stasis. A good example is *Pristiograptus dubius* (Suess), a conservative monograptid species which was the only survivor from the late Wenlock *lundgreni* Event. Soon afterward, it displayed a population explosion, occurring probably in huge populations (patches), which at the same time displayed an increase of both within-patch and between-patch variation. The role of numerical abundance and increased variation was twofold: on one hand it served to expand the niche, on the other, it produced some fabric that was used in later diversification into numerous daughter species and resulted in adaptive radiation (Fig. 1). The recovery of the graptolite fauna in the late Wenlock (Homerian) and early Ludlow (Gorstian) was based on the differentiation of this single survivor. It became the ancestor for the bulk of later graptolite faunas, all of which may be derived from this single indigeneous relic species. The role of immigration was negligible (Koren' and Urbanek, 1994, in press).

Initially, there were only two daughter species, which split from the *dubius* stem line as a result of the so-called early schism (Fig. 1). One of them — *Pristiograptus praedeubeli* gave rise to rather robust monograptids such as *Colonograptus* and *Saetograptus* (spinose monograptids of Gorstian stage). The second, *Pristiograptus idoneus* produced, via a generalized ancestral species *Lobograptus? sherrardae,* such diverse forms as *Neodiversograptus, Lobograptus* and probably also *Bohemograptus.* They display quite divergent trends of evolution but share a common ancestry.

At the same time the *dubius* lineage continued to exist without obvious morphological changes, though much less numerous. In my opinion, it should be treated as the same species and even the same subspecies (Fig. 2). This practice opposes the cladistic approach to the stem species — demanding that the ancestral species should be regarded as a new one, after each speciation commenced from it.
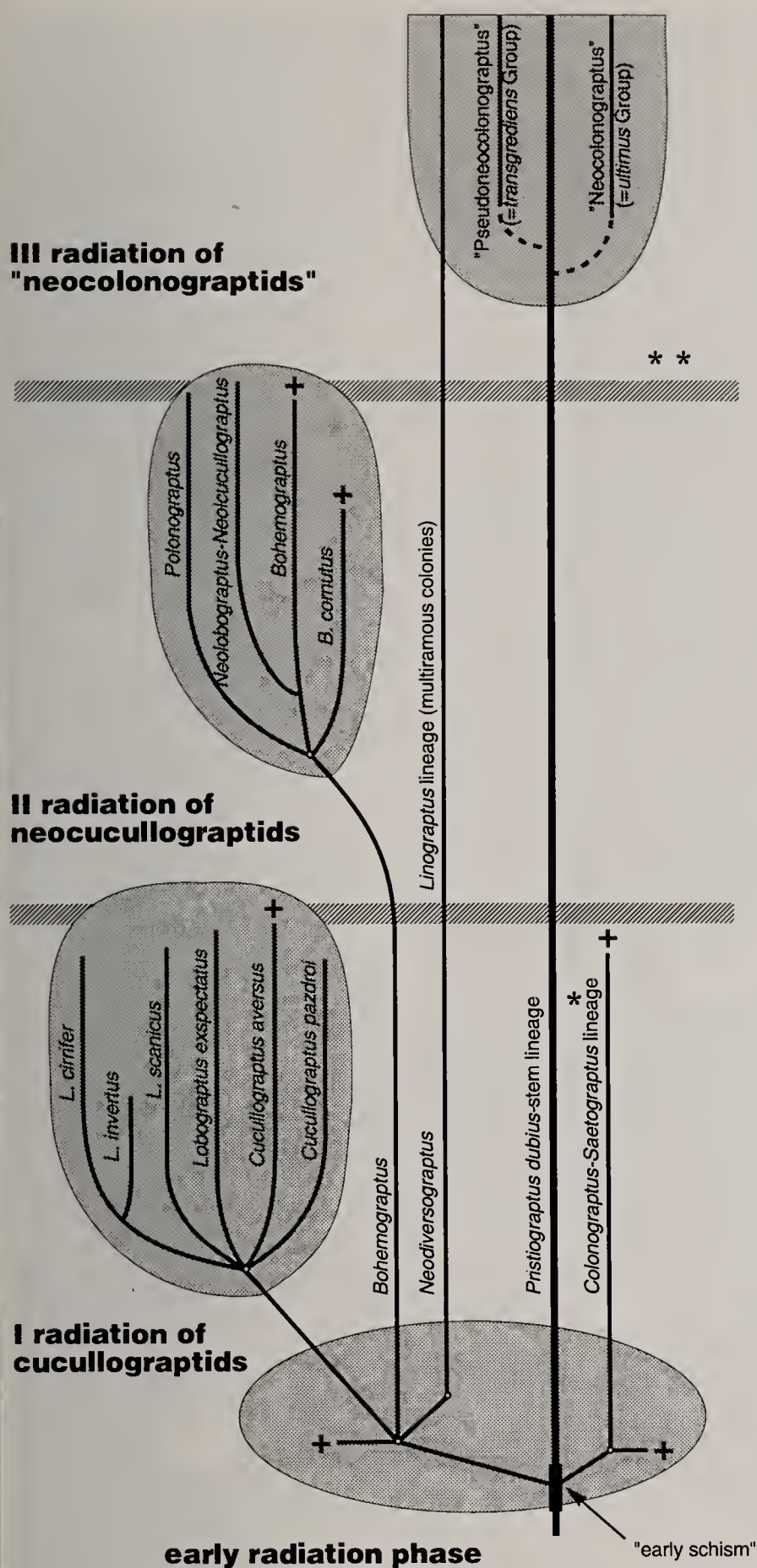
Fig. 2 - Phylogenetic relations among Upper Silurian monograptids, descendants of the *Pristiograptus dubius* (Suess) stem species. While the conservative stem lineage continues without obvious changes (thick line), its specialized derivatives (thin lines) are subject to strong diversification and common extinction. Note the heterochronous appearance of similar morphological types in Ludlow and Pridoli, namely *Colonograptus* and «neocolonograptids». Asterisks denote additional speciation from the *dubius* stem lineage: * *Pseudomonoclimacis dalejensis* (Bouček) in Gorstian time, ** *Pseudimonoclimacis latilobus* (Tseg.) and *Pristiograptus fragmentalis* (Bouček), both in Ludfordian. Wavy lines indicate main extinction events. The early radiation phase is shown at higher resolution on Fig. 1.

This is the «nodal principle» or the lineage concept of species in cladistic systematics, according to which the temporal duration of a species is determined by two processes of speciation, and species are «internodes» (segments of the phylogenetic tree; Hennig, 1966: 20; Bonde, 1981: 23). Hence, a species should be given different names before and after the speciation. Moreover, even strongly similar species are given different binomials if they are situated between different speciation events (nodes of the phylogenetic tree). This view is usually justified by the argument that because of the speciation the ancestral species completely changes its function in a phylogenetic system. In relation to the same daughter species, a given internode is considered to be ancestral before speciation and a sister species, after it. It seems obvious that one should not name the same entity now mother and now sister! In fact the latter argument is entirely unconvincing. It relies too literally on the analogy between genealogy and phylogeny – and this might be misleading. Giving such species as *Pristiograptus dubius* a different name before and after speciation because of purely formal reasons, is of course possible, but undesireable, in view of the parsimony of nomenclature, and moreover biologically unreasonable. Such a postulate also pays no attention to the fact that speciation does not always break the cohesion of the ancestral lineage (Simpson, 1951, Wiley 1978, 1979). In fact, stem species may survive one or more speciation events without a significant alteration. A good example is that of sticklebacks (*Gasterosteus*), described by Bell (1979), where morphologically divergent freshwater species were established on oceanic islands by the anadromous stock of *Gasterosteus aculeatus,* known since the Pliocene. Bell (1979: 87) is convinced that repeated speciation has not caused sufficient (if any!) alteration of the parental species during approximately 10 Ma, «to warrant regarding the latter as a succession of species».
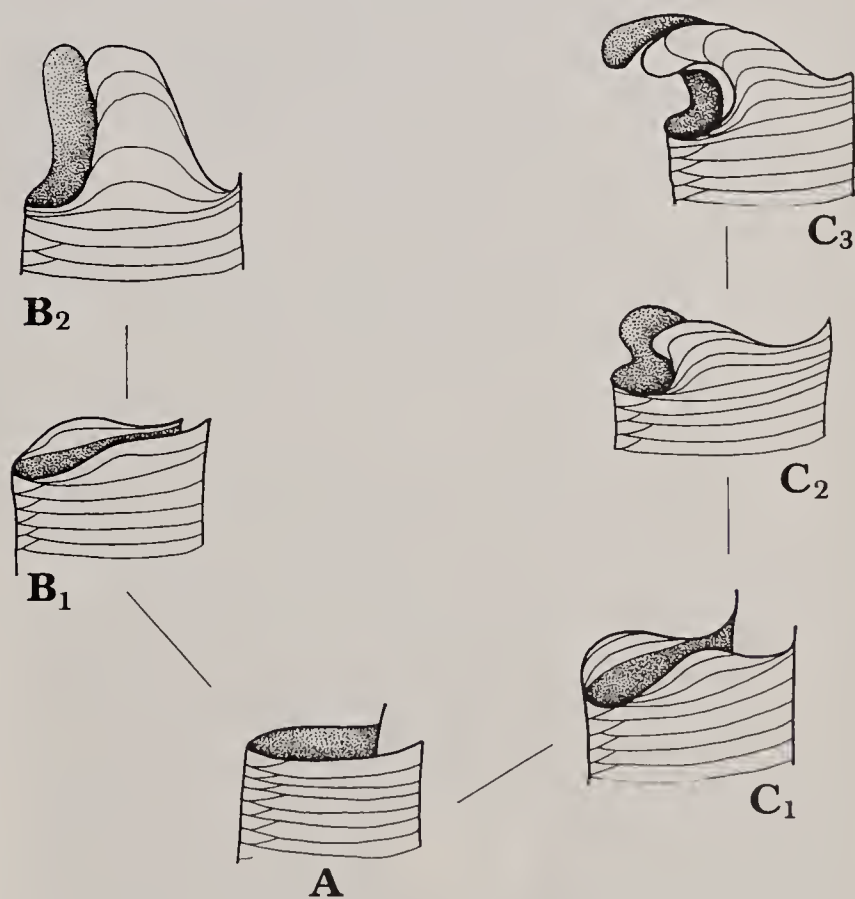
Fig. 3 - Comparison of the morphological evolution of bilateral apertural lobes in the proximal thecae of Ludlow colonograptids, as illustrated by «*Monograptus*» *praedeubeli* Jaeger (B_1, *praedeubeli* zone) and *Colonograptus colonus* (Barrande) (B_2, *nilssoni* Zone), with Pridoli «neocolonograptidis» represented by *Pseudomonoclimacis parultimus* (Jaeger) (C_1, *parultimus* Zone), *P. ultimus* (Perner) (C_2, *ultimus* Zone) and *P. lochkovensis* (Přibyl) (C_3, *lochkovensis* Zone). Final products (B_2 and C_3) display a remarkable resemblance, although they developed heterochronously and independently from the persistent stem lineage of *Pristiograptus dubius* with straight apertural margins (A).
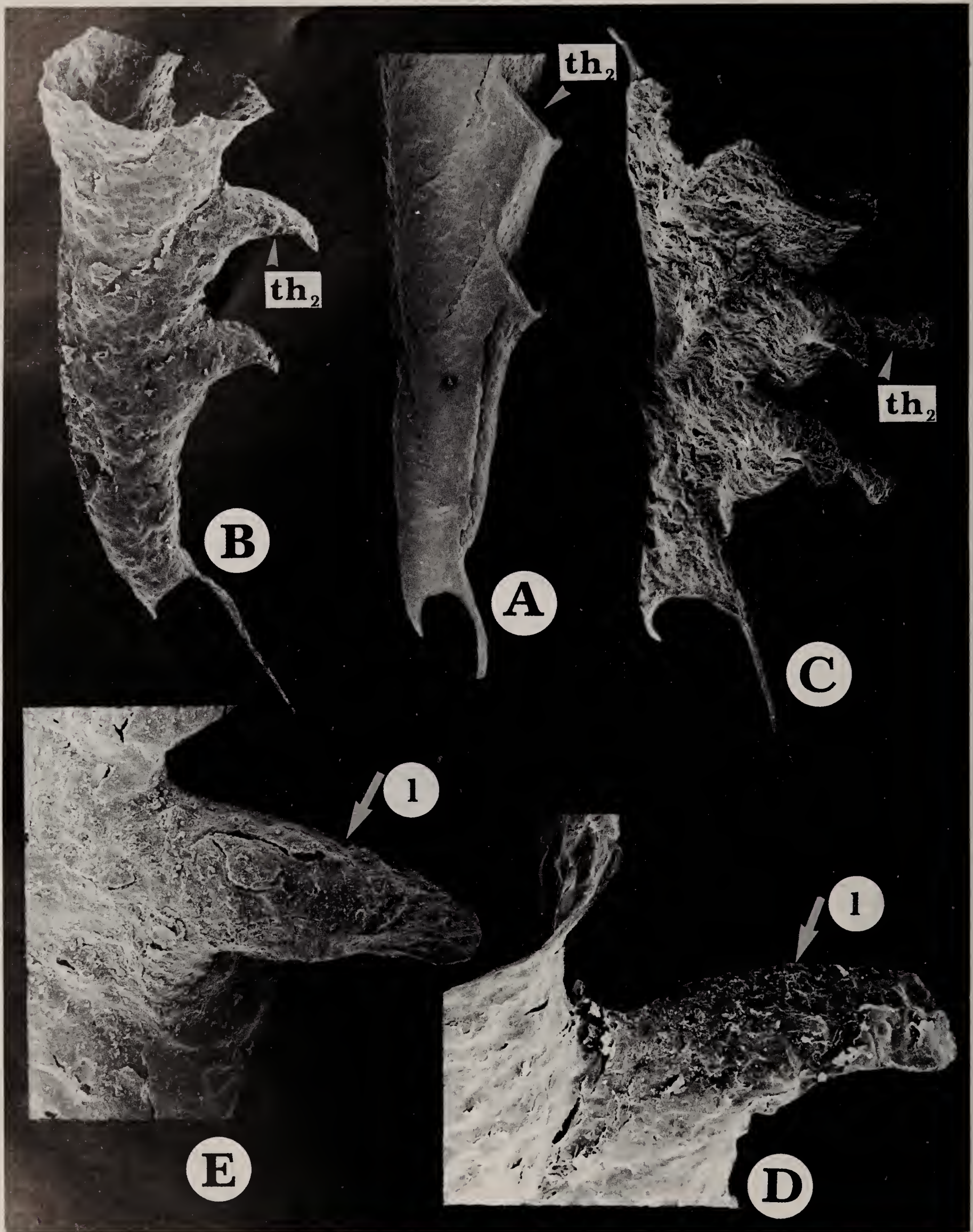
Fig. 4 - SEM micrographs showing proximal parts of A - *Pristiograptus dubius* (Suess), a conservative monograptid (Baltic erratic boulder, *parascanicus* Zone, Gorstian) and its descendants: B - *Colonograptus colonus* (Barrande), (Baltic erratic boulder, *nilssoni* Zone, Gorstian) as well as C - a «neocolonograptid» *Pseudomonoclimacis lochkovensis* (Přibyl) (deep boring, East European Platform, *lochkovensis* Zone). D-E - structural details of apertural lobes in B and C respectively. Taken with Philip XL 20 scanning electron microscope at 15 kV, from gold-platinum coated etched specimens. A-C × 50; D-E × 150.

Another argument frequently quoted by cladists is formulated in the following way: so much variation is lost in each speciation that this changes the entire evolutionary potential of the ancestral species. Empirical data do not confirm this assumption. *P. dubius* can be quoted as a historical experiment of a kind. After passing through a number of graptolite zones of Gorstian and Ludfordian age, the *dubius* stem lineage underwent a new (iterative) speciation in the early Pridoli time. The products were «neocolonograptids» — monograptids remarkably similar to the earlier Ludlow colonograptids (Fig. 3, 4), which had become extinct in the meantime (in the *leitwardinensis* Zone). Thus, provided that the niche is empty, the *dubius* stem species was perfectly capable of speciating iteratively in very much the same way as before. In other words, the *dubius* stem lineage featured essentially the same evolutionary potential during the Pridoli time (Fig. 3, C_1-C_3) as during the late Wenlock and Ludlow (Fig. 3, B_1-B_2), in spite of the numerous speciation events which occurred from the ancestral stock during this interval (Fig. 2).

The persistence of the stem species and the conservation of its evolutionary potential clearly contradicts the common conviction that speciation always means a total reorganization of the ancestral species. What we call «an historical experiment» indicates that at least in some cases such claims are contradicted by the data. Speciation events frequently do not affect the entire genetic pool of the ancestral species, but only a fraction of it. The entire genetic pool is affected when daughter species appear according to the «dumbbell» model of speciation, as defined by Mayr (1982), and when a parental species is suddivided into large derived portions. In fact, most of speciation events recorded among macrozooplankton belong to the category of parapatric speciation (van der Spoel, 1983; Boxshall, 1981). This mode of speciation involved only peripheral populations of the ancestral species, which later became semiisolated. Hence, the genetic loss for the entire system of the parental species was negligible. When analysing the *Gasterosteus* case, Bell (1979: 85) has arrived at a conclusion that «daughter speies neither carry away with them a significant unique portion of the species gene pool, nor outcompete... or alter the ecological niche of the parental species». The same was probably also true for the *dubius* lineage and expressed in the preservation of morphological spectrum and potential to change (Fig. 4, B-E). It should also be noted that the ecological niche of the *dubius* lineage, probably widened during the peak of numerical abundance, was later normalized without any considerable alteration. In spite of numerous oscillations in the prevailing morphotype of successive chronodemes, some samples of Pridoli age are remarkably similar to those of lower Ludlow age.

The persistence of the *dubius* stem lineage may only be approximately estimated, because of the relative scarcity of radiometric dating for the Upper Silurian as well as a large margin of uncertainty of each particular dating. Using the dated stratigraphic scale compiled by Odin and Odin (1990), one could estimate the age of the early schism as somewhat more than 420 Ma, and the appearance of first «neocolonograptids» as approximately 415 Ma (the bottom of the Pridoli). Therefore the *dubius* stem species preserved its evolutionary potential intact for at least 5 Ma and perhaps more!

An historical experiment - the case of spinose *Monograptus*

Another remarkable instance of a historical experiment is that of the lobate-spinose monograptids of late Wenlock and late Ludfordian age. The majority of late Wenlock monograptids (*M. flemingi, M. priodon*) had hooked apertural lobes as well as paired lateral spines (Fig. 5, B_1-B_2). Such monograptids became extinct during the *lundgreni* Event, and for some five graptolite zones the true monograptids - *Monograptus (Monograptus)* dissappeared from all known sequences in the epicontinental seas. They did not reapper until the *nilssoni* Zone, being represented by *Monograptus (M.) uncinatus* Tullberg. In contrast to the late Wenlock forms it is provided with an apertural lobe alone, without any spines (Fig. 5, A_1-A_2) and may be considered a derivative of the ancient nonspecialized stock rather than a survivor of the fauna immediately preceding the mass extinction which occurred towards the end of the Wenlock. *Monograptus (M.) uncinatus* soon disappears but similar forms reappear in the late Ludfordian and the early Pridoli. Thus the *uncinatus* lineage exhibits what is known as a classical «Lazarus effect», a pehomenon described by Jablonski (1986). After their final reappearance, *uncinatus*-like monograptidis play a very important role in Late Silurian and Early Devonian faunas. The great comeback of the true monograptids, represented by the *uncinatus* group, is one of the most remarkable features of late graptolite faunas. No wonder that they re-occupied the former *Monograptus* niche, which had been empty for some time, and made some «attempts» to fill it completely by producing again a lobate-spinose adaptive type, very similar to that encountered in the Wenlock (Fig. 5, C_1-C_2). Their main representative *Monograptus (M.) spineus* Tseg. may be derived from *Monograptus (M.) acer* Tseg., through a transient link yet undescribed. In this way we learn that the Ludfordian lobate-spinose species appeared independently of the earlier ones. Yet, they mimic them in their overall appearance, except for certain details. While the Wenlock forms have lateral spines situated postero-laterally, the Ludfordian ones have them in the antero-lateral position (Fig. 5, B-C). Comparing them with the ancestral structure of *Monograptus (M.) uncinatus* one may notice that the Wenlock species have their spines situated at point «x» and the Ludfordian ones, at point «y». This difference, however small, speaks for a somewhat «deficient» homology. Although in both cases the adaptive significance of the apertural apparatus thus attained is almost identical, minute details provide evidence for their independent, iterative origin. These spines are not merely non-identical, but they combine features of homolgy and homoplasy. Using Remane's (1956) widely accepted criteria of homology, namely: (1) position in a structural system, (2) specificity of structure, and (3) presence of transitional stages, one could conclude that the structures in question are basically homologous. This is because (1) in both cases spines are superimposed on the apertural lobe and (2) made of the same skeletal tissue, however, (3) they are not related to the same ancestral species, and they diverged at a different time producing different morphoclines. Thus we are dealing here with a border case between homology and homoplasy, the former being implied by

morphological criteria (1-2) of Remane (1956) and the latter by the phylogenetic aspect (criterion 3). A number of theoretical terms may be invoked here as relevant to a great or smaller extent, but neither seems fully adequate. As we are dealing here with the consequences of parallel evolution, structures in question may be defined as «homoiologous» (Plate, 1922; Remane, 1956). Usually their similarity is explained as a consequence of a certain potential derived from a common ancestor. This potential disposes them to change in a certain way, and they do so in distinct lineages (canalized evolutionary potential; Saether, 1983; Gosliner and Ghiselin, 1984). Structures produced in parallel or iterative lineages may reveal a deceptive combination of homology and homeomorphy, frequently beyond the resolving power of comparative-anatomical methods.

The above situation implies a certain philosophy. It is clear that the *uncinatus* stock preserved its evolutionary potential to form not only the apertural lobes but also spines. I am talking about a «potential» rather than about «tendencies» as proposed by Simpson (1961) in his classical definition of evolutionary species. A tendency is usually related to the internal factors of evolution, which produce change independently of the circumstances, whilst a potential can manifest itself only under certain conditions. I would also avoid such terms as «historical fate of the species» (as suggested by Wiley, 1978), which may imply a predeterministic nature of evolutionary change. G. G. Simpson usually viewed with caution autogenetic interpretations of evolution. However, when formulating his classical definition of species he seems to have forgotten about this danger.

The history and the iterative origin of the lobate-spinose monograptidis have much in common with the frequently debated problem of contingency of evolution, where «re-runs» of a certain sequence of events inevitably produce a different result each time. In our case, the Wenlock sequence and the Ludfordian re-run produced fairly similar, although not quite identical results. In recent debates the emphasis is usually put on the role of chance and on the unpredictability of results (Gould, 1989). The monograptid case reveals the role of deterministic factors and the essential repetition of results, although identity is not achieved. This increase in the significance of predictability is in an obvious way related to the amazing ability of the stem lineages to sustain their evolutionary potential through time in spite of numerous iterative speciations from the stem group. The morphogenetic dispositions are contingent rather than necessary but they persist long enough to produce the iterations.
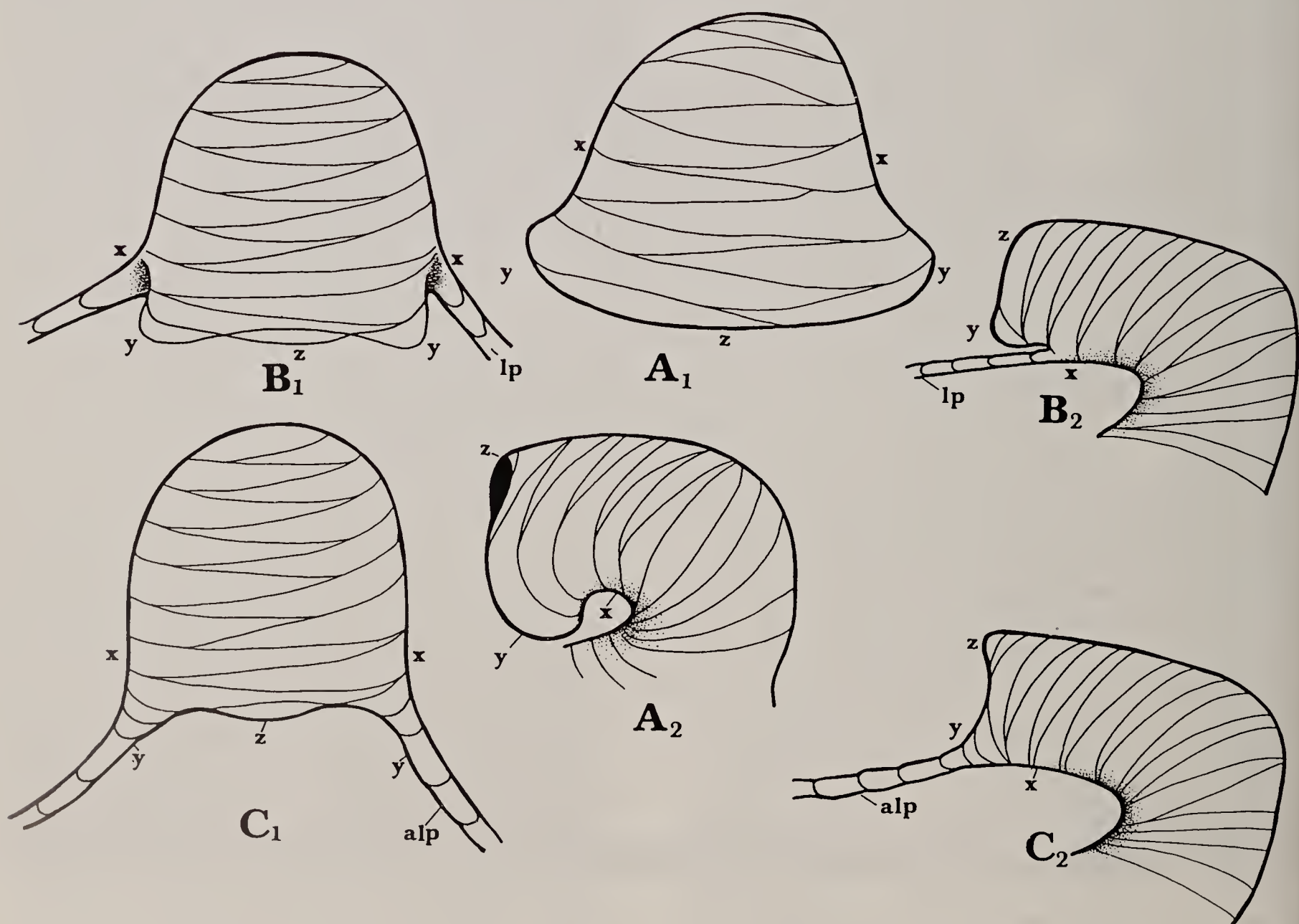
Fig. 5 - Comparison of apertural apparatus (A_1-A_2) in *Monograptus uncinatus* Tullberg from the *nilssoni* Zone (Ludlow, Gorstian) representing a nonspecialized, ancestral type of structure, with late Wenlock (B_1-B_2) and late Ludfordian (C_1-C_2) lobate-spinose monograptids. All seen in ventral and lateral aspects; x, y, z, homological points on the dorsal apertural lobe. Note that lateral processes (lp) in late Wenlock forms were situated at x, while their analogues (alp, anterolateral processes) in Ludfordian forms were placed at y. Point z was transformed in the latter group into a projecting edge (promontorium).

Adaptive radiations - generation and maintenance of diversity

The history of the Graptoloidea, planktonic graptolites, abounded in biotic crises, which strongly reduced the diversity of the fauna and placed the group on the brink of extinction. Since the end of the Ordovician, at least six such major crises have been distinguished, after which a strongly impoverished fauna displayed its ability to recover. As a rule, the recovery starts from indigeneous survivors which are subject to a population burst and then to growing diversification. The fossil record is complete enough to trace the extinction events and all the successive stages of recovery. In extreme cases, only one or two relic species undergo a population explosion producing huge patches of zooplankton. This is expressed taphonomically in the mass abundance of their fossil remains in the sediments or bedding planes (the so-called «graptolite carpets»). Such a population burst may be considered a direct response to the ecological release occurring due to the elimination of competing species and relaxation of the intra- as well as intergroup selection pressure. On the other hand, high numerical abundance creates suitable conditions for generation of genetic variation. This conclusion, first advanced by E. B. Ford (1931), was later developed into a common wisdom of evolutionary biology. No doubt, such increased variation is later used as raw material in both the forthcoming speciation and transpecific evolution.

Early phases of adaptive radiation are marked by a paucity of lineages that split off the ancestral species (Fig. 1). Moreover, the first representatives of the daughter lineages differ but little from the parental species. Nevertheless, they manifest different and frequently quite divergent trends of evolution. There appear numerous transients which frequently produce a complete spectrum of variation, from the standard ancestral morphotype to the morphotypes of newly-formed species. Their presence is a remarkable feature of this early phase of adaptive radiation. Some of the newly-appeared species, are forerunners of further successful and long-lasting trends (Fig. 2), some represent lines of precocious specialization and become extinct after a short period of success. The last named category produces blind alleys of phylogeny, while the former open avenues to much longer prosperity. This is especially true of those species which deserve to be named synthetic or generalized (terms frequently used in classical palaeontology). They combine incipient traits of specializazion, common to a number of descendant and completely divergent trends (Fig. 1). Such ancestral species as *Lobograptus? sherrardae* exhibit a great prospective evolutionary potential, which, however, could be estimated only retrospectively, and cannot be predicted from the morphology and stratigraphic occurrence of a given species. Some of the descendant lines are subject to secondary adaptive radiation. As far as the number of taxa produced is concerned, secondary radiation may surpass the primary one. However, these radiations are usually variations on a theme, as they represent modifications of a certain basic type and exploit the possibilities opened by the given adaptive type. Hence, their prospective potential is limited as compared with primary adaptive radiation (Fig. 2).

In many groups of graptoloids, and especially in the Monograptina, evolutionary changes were concentrated on certain key-features, namely on the apertural region related to the feeding apparatus of the zooid. The remaining structural features of the colony were affected to a much lesser extent or remain virtually unchanged. The evolution of such groups as the Cucullograptinae or Neocucullograptinae is a graphic example of the significance of trophic specialization for the generation of diversity. The evolution of particular lineages exhibits a remarkable advance in the improvement of a particular adaptive type (fig. 5). The replacement of sequential chronospecies within such lineages accounts for a growing degree of structural elaboration and possible sophistication of the feeding mechanism. This is an obvious instance of an anagenetic trend in the phyletic evolution of a single line of descent.

The co-existence of a number of species representing a basically similar adaptive type may be ensured by the generation of character differences between related species. This seems to be particularly true of plankton where, paradoxically, a number of congeneric species may co-exist sympatrically. Hutchinson (1959, 1961) suggested an explanation of this «paradox of plankton», assuming that there exists a certain safe limit of character differences in the trophic apparatus (a difference in size by a 1.3 ratio!). Such a magnitude of differences allows a subdivision of the trophic niche and correspondingly a relaxation of competition. At the same time, such character differences permit many species to co-exist and avoid replacement, inevitable in view of the action of Gauze's principle.

The family tree of many monograptids provides convincing evidence that generation of differences between closely related species with a largely similar adaptive type played an important role in evolution. This factor was also responsible for cladogenesis — diversification into numerous independent evolutionary lines. One could hardly escape the conclusion that generation of character differences was the primary effect of evolutionary changes, as differences *per se* had a positive effect on the survival of the species and the stability of the ecosystem (Fig. 6).

The later and more advanced species of the majority of the lineages represent, in most graptoloid groups, K-strategists (as defined by McArthur and Wilson, 1967). They were adapted for exploitation of a certain, rather narrowly defined fraction of food resources and possess elaborated and sometimes bizarre apertural devices. However, in the early stages of recovery, the ancestral species displayed a lack of trophic specialization (frequently no apertural structures at all) as well as some other features of r-strategies. Both the transition from the r- to the K-strategy and the numerical increase of diversity and morphological complexity are side-effects of the best known adaptive radiations. This process was punctuated from time to time by planetary disturbances of the environment resulting in mass extinctions. They, in turn, were followed again by a recovery and re-radiation (Fig. 2). From the standpoint of evolutionary ecology, the Graptoloidea behaved as the famous Russian doll — «Van'ka-vstan'ka» (literally «Johnnie, keep standing!»). It has a weight attached to its rounded base causing it always to recover its stand-

Fig. 6 - Morphological effects od adaptive radiation in Upper Silurian monograptids of the subfamily Cucullograptinae, as exhibited by the sicula and the first theca of the colony. 1 - *Lobograptus progenitor* Urbanek, the stem species of the group; 2 - *L. simplex* Urbanek, the central species within the subfamily and a generalized ancestor for divergent lines; 3 - *L. expectatus* Urbanek, an advanced but still symmetric lobograptid; 4 - *L. scanicus parascanicus* (Kuhne); 5 - *L. scanicus amphirostris* Urbanek; 6 - *L. scanicus scanicus* (Tullberg); 7 - *L. imitator* Urbanek; 8 - *L. invertus* Urbanek; 9 - *L. cirrifer* Urbanek; 10 - *Cucullograptus hemiaversus* Urbanek; 11 - *C. aversus rostratus* Urbanek; 12 - *C. pazdroi* Urbanek. Heavy arrows indicate a presumable direction of evolution in symmetric lobograptids, whilst thin arrows show the same in other lineages. Note that 4-9 display hypertrophy of the right lobe and 10-12 display hypertrophy of the left lobe, a - indicates the obverse (left) aspect of the aperture in asymmetric species (after Urbanek 1966, modified).

ing position. However, after one of the bends something got wrong with the toy itself — it never rose up again. These problems, however, are beyond the scope of the present contribution.

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Schmalhausen's evolutionary morphology and its value in formulating research strategies

Abstract – Schmalhausen (1884-1963) made important contributions to several biological fields, notably embryology, evolutionary morphology, and evolution. Had his important work on stabilizing selection been available to western biologists at the time of the «evolutionary synthesis» it is likely that he would be seen as one of its important architects. His early work as an experimental embryologist contributed to his development of the concepts of norm of reaction and phenotypic plasticity as important components of evolutionary studies. Brief examples from recent studies of limb and brain evolution in amphibians show how his work retains relevance for formulating research programs.

It is my contention that the great Russian biologist I. I. Schmalhausen (1884-1963), was far ahead of his time in his approach to problems in evolutionary morphology. Contemporaries such as Dobzhansky (1949) knew and appreciated him, but he was mainly ignored by other western biologists, even including Waddington, whose work paralleled that of Schmalhausen in some important respects. Here I review some of Schmalhausen's main contributions and show how his approach has relevance for developing modern research strategies in evolutionary morphology.

Elsewhere (Wake, 1986) I have presented an overview and perspective on one of the two books by Schmalhausen (Factors of Evolution, The Theory of Stabilizing Selection, 1949) that have been translated into English. It is regrettable that more of his work is not readily accessible to western readers, for even the most famous of his books in Russian (Schmalhausen, 1969) remains untranslated. Increased attention has been accorded to Schmalhausen recently, including a biography by his daughter (Schmalhausen, 1988) and interpretations of his scientific approach to evolutionary studies (Allen, 1991; Vorobyeva, 1992). I present only some highlights, derived from Schmalhausen's own work and from the sources cited above (and papers cited in turn by them) that are of special relevance to points I will make in this paper.

Schmalhausen and his Contributions

Ivan Ivanovitch Schmalhausen was a student of the famous comparative anatomist A. N. Severtsov, one of the first true evolutionary morphologists (Adam, 1980). Severtsov was interested in general rules of morphological development and evolutionary transitions in morphology; that is, in regularities, repeated patterns and parallels between ontogeny and phylogeny. These issues were united in a field that he termed «phyloembryogenesis». Schmalhausens's earliest work dealt with comparative studies of limb and fin development in anurans, urodeles, mammals and fishes (Schmalhausen, 1907, 1908a, 1908b, 1910, 1912), and his contributions have been of lasting value.

Schmalhausen was educated as a comparative embryologist and anatomist, and he remained associated with these areas of inquiry throughout the first part of the century. The early part of Schmalhausen's professional career was an intellectually stimulating time for Russian evolutionary biology. He was a contemporary of Chetverikov, whose early studies of geographic genetic variation led to a long-continued tradition and strong point in Russian biology. This was the intellectual environment that also produced Dobzhansky. A prevalent theme was that there was a great store of genetic variation in populations and that populations simply absorbed mutations that came along steadily. Also important was Vavilov, a great botanist whose work is more appreciated now than in the past, and who studied the evolutionary origins of domesticated plants. Vavilov was especially interested in regularities in patterns of plant evolution, and is responsible for the so-called «laws» of homologous series (e.g., Vavilov, 1922). I consider Vavilov to be the father of modern studies of homoplasy.

It was perhaps inevitable that a morphologist interested in evolution would also become interested in the genetic foundation of morphological variation, and Schmalhausen became increasingly recognized, within Russia, as a general evolutionary biologist. He succeeded his old professor as director of an institute in Moscow in 1936, and eventually became Professor of Darwinism in the University of Moscow.

It was Schmalhausen's great misfortune to work during a period of great political uncertainty and tumult. Both Chetverikov and Vavilov suffered political ostracism, and Vavilov disappeared. Schmalhausen himself was denounced during the period of the ascendency of Lysenko and attacks on mendelian genetics in the late 1940's, and he was removed from his professorship (Zirkle, 1949). He was partially rehabilitated later, on condition that he restrict himself to studies of comparative embryology and morphology and avoid genetics. The laboratory he then developed in Moscow made important contributions to our understanding of comparative morphogenesis of vertebrates.

The work that introduced Schmalhausen to the English-speaking community of evolutionary biolo-

gists is «Factors of Evolution», translated from the earlier Russian version and published in 1949. This book was written during the Second World War, when Russia was out of touch with developments in the West, and even its publication in Russian was delayed until 1947 (the Russian version is dated 1946, but Dobzhansky [in Schmalhausen, 1949] states that it did not appear until 1947). So, when it reached American and British scientists it appeared to be dated, with few modern references. Despite a laudatory introduction by Dobzhansky, the book really had no immediate impact. It did not even cite Simpson or Mayr, so one can imagine how it was received by these scientists, who considered themselves to be the architects of «The New Synthesis» (Mayr and Provine, 1980); it was largely ignored.

Many of the topics addressed by Schmalhausen are of great interest today: norms of reaction, phenotypic plasticity, morphological stasis, and morphological transitions are just a few of the major items (e.g., Sultan, 1992). I think of his book as the most comprehensive and even the most lasting of the great works of the period of the modern synthesis (that is, of the books published from the late 1930's through the 1950's). Allen (1991) has characterized Schmalhausen's work as that of a true, practicing *dialectical* materialist (as contrasted with a *mechanistic* materialist such as R. A. Fisher and perhaps most western evolutionary biologists). The fusion of mendelian genetics with darwinian natural selection led to a focus on genes and to the reduction of issues once thought to be organismal in nature into component parts. The general assumption of the mechanistic materialists was that the whole is equal to the sum of its parts, with no emergent qualities. Thus, in neodarwinism there is emphasis on environmental change, and on atomistic phenomena that frequently are seen as parts of a mosaic of separate and interacting, but ultimately independent, parts. In contrast, the dialectical materialist position of Schmalhausen (enjoying a current resurgence, although most practitioners are unconscious of the philosophical underpinning) sees the parts so interconnected that they cannot be studied separately (Sewell Wright certainly would have been comfortable with this). Change is seen as a fundamental part of any system; it is not necessarily imposed by outside phenomena but rather is built into the interaction of parts, that is, it is an expected outcome of the organization of the system. The internal forces of change can be understood as interactions of factors that are fundamentally in opposition, but are nonetheless components of the system. Thus, on the one hand, heredity is conservative, while on the other, variation is inevitable and radical in its possibilities. Evolution is the outcome of what might be viewed as the opposing forces of heredity and variation. Furthermore, quantitative changes always lead eventually to qualitative change, so that novelty is an expectation. This can be seen most clearly in the processes associated with allopatric speciation, where quantitative changes eventually result in the qualitative change of reproductive incompatibility. In all of this, historical contigency plays a central role.

Allen (1991) has argued that Schmalhausen was a committed dialectician, not a cosmetic one who was conforming to a prevailing political system. In support of this view, Allen cites Schmalhausen's continuous emphasis on the contradictory forces involved in evolution, and his attempt at a true synthesis between genetics and evolution theory, on the one hand, and embryology (and I would add morphology) on the other. Schmalhausen's dialectical approach is especially clear in his focus on stabilizing and dynamic selection as opposing forces; in fact, one can logically argue that Schmalhausen more than anyone else first presented a full theory of stabilizing selection. In his world view, stabilizing selection simply had to be emphasized.

I assert that the development and utilization of the concept of the norm of reaction has been one of Schamalhausen's most lasting contributions. A norm of reaction is the range of phenotypic expression of a given genotype. Schmalhausen recognized stable (genetically fixed, in essence, and highly predictable) and labile («morphoses» and modifications) traits. Morphoses (or phenocopies, features which are indicative of the potential of the developmental system, and hence also predictable) and modifications, which he thought of as at least potentially adaptive, both usually fall outside the norm of reaction of a genotype, except that some categories of modifications could be within the norm. Stabilizing selection converts labile into stable traits. Selection on morphogenetic processes leads to the internalization of external cues, which stabilizes development and makes outcomes highly predictable. Clearly there is a hierarchical component in this. In a variable environment, norms of reaction change constantly, as stabilizing selection does its work. Viewed in a modern perspective, what is needed is a phylogenetic interpretation of the evolution of norms of reaction, for then we will be able to reach a true synthesis of homoplasy and directional evolution.

Schmalhausen used many examples to show that he was thoroughly familiar with then-current genetics, evolutionary theory, development, comparative anatomy, and paleontology. He attempted a synthesis that was both prescient and extraordinarily perceptive. Regrettably, a truly modern synthesis still eludes us, and it is unclear to me whether this is because we lack sufficient empiricism (the almost daily discoveries in developmental genetics continue to be stunning in their possible implications), or because we cannot see the forest for the trees.

My own research has been influenced by that of Schmalhausen in a number of ways, and I will cite two examples that show how his perspectives shaped my work. The first of these focuses on trait evolution, and indirectly relates to morphoses, modifications, and norms of reaction. The second relates to hierarchical issues in organismal and taxic evolution, and the relation between parts and wholes.

Limb Evolution in Urodeles

Some of Schmalhausen's earliest work dealt with limb development in salamanders. His interest was mainly in morphogenesis, but he was strongly influenced by the classic comparative anatomy practiced in Europe in the early part of this century and therefore framed his study phylogenetically. He was especially interested in the relation of parts to wholes with respect to limbs, in particular, the organization

of the mesopodial region, the carpus and tarsus. The mesopodia of salamanders contain a number of elements that arise as mesenchymal condensations which chondrify and, in some taxa, ossify. Development of the region involves segmentation and bifurcation of axes of condensation (for a modern review see Shubin and Alberch, 1986). Two of these axes arise as segmentations (preaxial) and bifurcations (postaxial) from the rudimentary distal long bones (radius and ulna in the forelimb; tibia and fibula in the hindlimb). These axes grow from a proximal origin distally during development. A third arises as an independent distal condensation (preaxial), which spreads postaxially, segmenting and bifurcating to form the digital arch (ultimately giving rise to the distal mesopodials, the metapodials and the digits). The three axes converge in the central postaxial region, where Schmalhausen noted a recurrent variant pattern, the appearance of an additional central element (called by him mediale 3, and hence known to workers in the field as «Schmalhausen's m»). He argued that this element is in the background, so to speak, of the generative dynamics of the limb, and that it can variously be present as a separate element, as an amalgamation with a central tarsal, or as an amalgamation with a distal tarsal. Thus, he was exploring generative rules of development and both the bounds on phenotypic expression and the opportunities presented for the evolution of novelty. This research clearly influenced his later important work on phenotypic plasticity, stabilizing selection, and hierarchical issues in evolutionary biology.

Recently Neil Shubin and I have been exploring patterns of variation in salamander limb development from a phylogenetic perspective. In one recently completed study (coauthored with Andrew Crawford) we examined a large series of specimens of the newt *Taricha granulosa,* collected from a single pond in California that had unexpectedly frozen solid and killed the newts. We examined 452 skeletons, and found that about 95% of the forelimbs and 89% of the hindlimbs has the expected, «standard» organizational pattern of the mesopodials. An enormous number of combinations fusion or separation of the seven carpal and nine tarsal elements can be conceived, but we encountered only 21 carpal and eleven tarsal patterns. We found that five patterns were bilaterally symmetrical, which implies an organismal basis (as opposed to a local developmental irregularity). By far the most common of these patterns, both absolutely and in a symmetrical state, was Schmalhausens's m (in 5.4% of hindlimbs, and as a symmetrical pattern in both hindlimbs in 2.0% of individuals). A phylogenetic analysis disclosed that the presence of m as a discrete element restores an ancestral character, found both in fossil temnospondyls and in basal outgroups among salamander taxa. Thus, m is a phylogenetic atavism, the reappearance of a trait characteristic of ancestral taxa. One other symmetrical state also is an atavism. The three remaining symmetrical states duplicate patterns found elsewhere among urodeles either as rare variants or as fixed, novel, apomorphic states. Interestingly, m plays a role in three of the five most common patterns, either as a free-standing atavism or as a part of an amalgamation that has biomechanical and hence possibly adaptive significance. The apomorphies are morphological novelties that have been related to both developmental and adaptive processes (e.g., Wake, 1991). The critical point is that all of the variants are familiar; evolution tends to run in grooves, with generative processes channeling phenotypic expression. The bounded patterns of variation are the manifestation of a combination of phylogenetic history and developmental constraints. What ultimately becomes fixed in a clade may well represent the working of natural selection on the underlying variation. The variant patterns appear as complete and integrated alternative states, and the selection pressures leading to their fixation could be very weak. Once fixed, the new patterns might be very important, and in hindsight viewed as key innovations which open new possibilities for evolutionary diversification (Larson et al., 1981; Wake and Larson, 1987; Wake, 1991).

Brain Evolution in Urodeles

Brains of salamanders historically have been viewed as very generalized, and many neuroanatomists have referred to them as primitive. Others have observed that they appear to be developmentally relatively undifferentiated. However, there clearly is something wrong with this observation, for in many respects the brains of chondrichthyans and even those of petromyzontids are anatomically more complex than those of salamanders. Furthermore, several parts of the teleost brain are vastly more complex (e. g., the cerebellum) than those of salamanders. So, on phylogenetic grounds it is clear that the salamander brain is secondarily simplified (Roth et al., 1993). In collaboration with G. Roth, K. Nishikawa and others in their laboratories and mine, we have been exploring the reasons for this simplification. It now seems clear that salamanders are, in essence, caught in a phylogenetic and evolutionary trap. On the one hand, they have extraordinarily large genomes, and having large genomes means having large cells (Session and Larson, 1987. On the other hand, they are relatively small vertebrates, and some of them are very small, perhaps the smallest tetrapods; this means that they have to produce a complicated brain in a small space with very large cells, and so something has to give. Neuron packing is nearly as tight as it can be, and there is little glial matter in the smallest species (Roth et al., 1990). The extreme cases of brain simplification are found in salamanders of very small size (several species mature at body sizes less than 20 mm) with the largest genomes and cells. I have argued (Hanken and Wake, 1993) that these small salamanders are biologically very much smaller than their metric size implies, and when comparing taxa that vary greatly in cell size, metric size inappropriately and inadequately expresses biological size. Recently we found that large genomes also mean morphological simplification of brain organization in two other vertebrate clades, frogs and dipnoans (Roth et al., 1994).

Brain organization in amphibians illustrates well the significance of hierarchical factors (relation of molecules, cells, organs and organisms) in evolution. In addition, it shows how misleading it can be to consider isolated parts outside of the context of the whole. It is far more parsimonious to interpret the

overall organization of the brain as being directly related to cell size than it is to generate a series of separate explanations for the simplified organization of one part after the other.

Summary

Schmalhausen developed a perspective toward evolutionary biology that is resoundingly modern. He was a through-going darwinian, who understood natural selection theory and applied externalist perspectives throughout his career, but at the same time he was a well trained embryologist who understood the nature of generative rules and interpreted them in an evolutionary framework. Evolutionary developmental biology is only one field that owes Schmalhausen a debt. His contributions were general, in that they dealt with all of organismal evolutionary biology, and I believe that they will be some of the most long-lasting contributions from the period of the late 1930's and early 1940's. During the last decade, and continuing to the present, there has been a rebirth of interest in many of the issues Schmalhausen first raised.

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MEMORIE

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Volume XXVII - Fascicolo II

STUDI GEOBOTANICI ED ENTOMOFAUNISTICI NEL PARCO REGIONALE DEL MONTE BARRO

A cura di
CARLO LEONARDI E DAVIDE SASSI

MILANO 17 DICEMBRE 1997

Elenco delle Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano

Studi geobotanici ed entomofaunistici nel Parco Regionale del Monte Barro

a cura di
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Volume XXVII - Fascicolo II

17 Dicembre 1997

Memorie della Società Italiana di Scienze Naturali e del Museo Civico di Storia Naturale di Milano

INTRODUZIONE

Pur essendo di limitata estensione, il Parco del Monte Barro, istituito dalla Regione Lombardia con legge n. 78 del 16 settembre 1983, presenta un elevato interesse paesaggistico, geologico e naturalistico, in particolare per quanto riguarda la flora (che comprende numerosi endemismi) e la vegetazione.

In considerazione del fatto che, malgrado le peculiarità di questo Parco, la sua entomofauna risultava praticamente sconosciuta, il Museo di Storia Naturale di Milano si è posto l'obbiettivo di colmare, sia pur in modo molto parziale, tale lacuna, effettuando in quest'area, con un Contributo economico che il Parco ha concesso alla Società Italiana di Scienze Naturali, una serie di raccolte negli anni 1989-1992. Il censimento faunistico, inizialmente finalizzato allo studio dei Coleotteri Crisomelidi, è stato successivamente esteso ad altri gruppi di insetti, prevalentemente o esclusivamente fitofagi, e ai ragni; sul cospicuo materiale raccolto si basano i lavori riuniti in questo volume.

La nostra più viva riconoscenza va al Presidente e al Direttore del Consorzio Parco Monte Barro, Prof. Giuseppe Panzeri e Dr. Mauro Villa, che fin dall'inizio hanno appoggiato questo progetto.

Carlo Leonardi & Davide Sassi

Enrico Banfi, Gabriele Galasso & Davide Sassi

Aspetti floristico - vegetazionali del Monte Barro (Prealpi di Lecco) in relazione all'area delle raccolte entomologiche

Riassunto - È stata studiata la flora di 9 stazioni di ambiente aperto nell'area del Parco del Monte Barro, con particolare riguardo per gli aspetti sistematico-tassonomici e corologici, dai quali è emersa la necessità di una revisione critica globale della flora dell'intero territorio del Barro. Tale ricerca, servita di supporto a una più vasta indagine entomologica, ha messo in evidenza aspetti della vegetazione, ufficialmente già noti, la cui interpretazione tuttavia potrà essere modificata o migliorata da una più esatta conoscenza della flora; ciò anche nella prospettiva di acquisire le basi per una valutazione attendibile della biodiversità dell'intero territorio.

Abstract - Floristic and vegetational aspects of Mt. Barro (Italy, Lombardy, Prealps of Lecco) referring to the area of the entomological sampling.

The flora of Mt Barro has been already investigated in the past. A detailed floristic analysis of 9 meadow samples, recently accomplished to support an entomological research which has been carried out by the Natural History Museum of Milano, has evidenced interesting systematic-taxonomic and phytogeographic data. These observations lead the authors to consider the necessity of examining again the flora of the whole territory on the basis of modern knowledge and concepts, especially in order to throw light on the biodiversity and to determine its consistence. Furthermore the vegetation is taken into account to identify plant communities of sampling sites 1-8. Phytodiversity has been evaluated by using k-dominance and diversity Shannon parameters.

Key words: Mt. Barro, Flora, Vegetation.

Il Monte Barro è un piccolo massiccio calcareo costituito prevalentemente da bancate di Dolomia norica, prospicente il versante sudorientale (Monte Moregallo, Monte Rai, Corni di Canzo) dei rilievi del cosiddetto Triangolo Lariano e da questo separato mediante l'ampia depressione alluvionale della Val Madrera. Direttamente affacciato a oriente sul Lario lecchese, determina, con le sue pendici settentrionali, la separazione di questo dal piccolo bacino di Garlate, segnando l'inizio della valle dell'Adda postlariana.

È strutturalmente e morfologicamente connesso con la piccola catena dei Colli Briantei che, allungata in direzione nord-sud, costituisce per una quindicina di chilometri lo spartiacque tra la valle del Lambro, a occidente, e il corso dell'Adda, a oriente.

Pur non segnando, con la sua cima, una quota particolarmente elevata, 922 m, il Monte Barro possiede notevoli motivi di interesse geomorfologico e floristico. Durante le fasi di maggiore espansione dei ghiacci pleistocenici, l'intera superficie, a eccezione della vetta e di alcune anticime poste a meridione di essa, fu ricoperta dai ghiacci che, oltre a lasciare profonde tracce sulla morfologia del territorio, cancellarono ogni forma di vegetazione. L'attuale flora è dunque di formazione recente, essendosi ricostituita a partire dall'ultimo interglaciale.

La particolare posizione strategica del Monte Barro, isolato dai rilievi circostanti e affacciato a sud sulla vasta pianura briantea, fu sfruttata in epoca storica dai Romani e, successivamente, dai Goti, che vi costituirono vari nuclei di insediamento, databili al V-VI sec. d. C., a tutt'oggi soltanto in parte esplorati. Una serie di campagne di scavi, condotte regolarmente in questi ultimi anni, ha portato al ritrovamento di reperti di notevole interesse.

Vista dunque la grande importanza, sia naturalistica che storica, del Monte Barro, fu istituito con la legge regionale 16 settembre 1983, n. 78 il Parco naturale del Monte Barro, esteso su una superficie di 665 ettari.

Il Monte Barro è costituito da formazioni carbonatiche, la cui età si estende dal Norico al Cretaceo medio-superiore, formanti una serie di quattro grosse scaglie, disposte in successione nord-sud, subverticali o immerse grosso modo verso nord (Nangeroni, 1972). Si tratta di una prima fascia di Dolomia Principale (Norico), affiorante lungo le pendici settentrionali fino ad un piccolo sperone roccioso posto a quota 858 m; segue una fascia di calcari marnosi del Retico medio-inferiore, comprendente l'intera Val Faè e la regione della vetta, a esclusione delle roccette della sommità, costituite di Dolomia Conchodon (Retico superiore); una terza scaglia, ancora in Dolomia norica, e infine una quarta fascia, costituente tutto il basso versante meridionale, formata da calcari marnoso-selciferi liassici (Calcare di Moltrasio), calcari del Giurassico sommitale e del Cretaceo inferiore (Maiolica), e marne e arenarie del Cretaceo medio-superiore.

Da un punto di vista strutturale, il rilievo è interessato da due anticlinali parallele, ad asse disposto in direzione NO-SE. Tra di esse trovasi la sinclinale della Val Faè, la quale, determinando l'affioramento dei teneri calcari marnosi del Retico medio-inferiore, incassati tra la prima e la seconda scaglia di Dolomia norica e separati da esse da due notevoli faglie, si trova in evidente concordanza morfologica con la topografia.

La morfologia, oltre che delle condizioni strutturali e meteorologiche, risente in misura evidente, nei depositi, nel modellamento e nell'erosione, dell'azione sviluppata dai ghiacci. Depositi morenici, rocce levigate e striate, erratici anche di notevoli dimensioni, generalmente in ghiandone della Val Masino, sono rinvenibili fino a quota 874 m, segnando il limite della copertura dei ghiacci quaternari.

Potenti bancate di depositi fluvioglaciali, generalmente sottoposti a morenico, in gran parte trasformati in cave di sabbia, sono visibili lungo i bassi versanti settentrionali. Piuttosto marcato appare in alcune zone il modellamento carsico superficiale: per esempio l'ampia balconata rappresentata dal Pian Sciresa è probabilmente un vasto polje, costellato nella zona meridionale da piccoli rilievi residuali a sommità tondeggiante tipo hum.

Il clima

La massa idrica del lago di Lecco, unitamente a quella degli altri corpi d'acqua più piccoli che circondano a est e a ovest il Monte Barro, determina il carattere spiccatamente oceanico del clima di questo territorio. D'estate l'aria satura di umidità sale nelle ore più calde e si espande raffreddandosi per poi scaricarsi ostacolata dai contrafforti montuosi. I dati termopluviometrici sono stati forniti dal Consorzio dell'Adda, provengono dalla stazione di Olginate e si riferiscono al periodo 1981-1991 e alla quota di 206 m s.l.m.; per quote superiori è necessaria una piccola correzione lineare in abbassamento dei valori termometrici secondo il gradiente termico altitudinale (Belloni & Pelfini, 1987). Le precipitazioni annuali sono tra le più elevate del settore prealpino, 1.300 mm, con punte ben superiori in certe annate (1.678 mm nel 1984; il minimo si è avuto nel 1983 con 993 mm); anche l'umidità relativa è sempre molto alta e nelle giornate più asciutte raramente scende sotto il 70%. In compenso la media termica annuale è di 13°C e la temperatura del mese più freddo rimane leggermente sopra 3°C, sempre grazie all'effetto tamponante del sistema lacustre. Il gradiente termico verticale negativo per il dislivello 206-922 m s.l.m. comporta un aumento con la quota delle probabilità di gelate, nevicate e permanenza del manto nevoso; il climogramma secondo Bagnouls-Gaussen (Fig. 1) consente di inquadrare la tipologia climatica del nostro territorio nella regione mesaxerica, sottoregione ipomesaxerica, tipo C(10) insubrico (Tomaselli et al., 1973), caratterizzato fra l'altro da assenza di deficit idrico estivo. Considerando che il Monte Barro è circondato da montagne più alte (Corni di Canzo, 1373 m; Moregallo, 1276 m; Resegone, 1875 m; Albenza, 1250 m) costituenti la barriera effettiva alle masse d'aria umida, si può ritenere che la variazione delle precipitazioni con la quota non sia significativa. Pertanto è lecito riferire
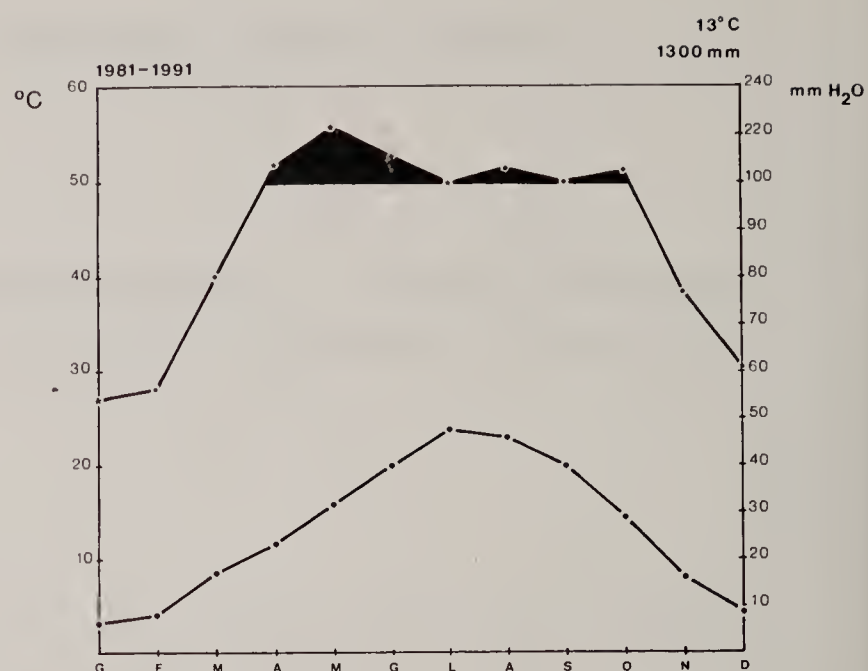
Fig. 1 - Climogramma secondo Bagnouls-Gaussen basato sui dati termopluviometrici della stazione di Olginate (1981-1991).

tutti i valori di continentalità igrica (indice di Gams) al totale annuo di 1.300 mm; ne deriva che dalla stazione di Olginate alla vetta del Barro l'indice varia tra 9° e 35°, in evidente accordo con le caratteristiche oceaniche del clima.

Un punto degno di nota è l'inversione termica che contrassegna i versanti del Monte Barro caratterizzati da una componente in esposizione meridionale: infatti, in media, sotto i 500 m di quota prevalgono formazioni a tendenza più microterma (*Carpinion, Tilio-Acerion*) di quelle sovrastanti (*Quercion pubescenti-petraeae*); a sud la roverella giunge quasi in vetta (850 m) dimostrando gli effetti microclimatici determinanti della buona esposizione.

Aspetti generali della vegetazione

Nel corso di una pluriennale serie di ricerche, svolte dal personale scientifico del Museo di Storia Naturale di Milano, e orientate prevalentemente allo studio dell'entomofauna del Monte Barro, sono state condotte osservazioni sulla vegetazione e sulla flora, in particolare su quest'ultima, a seguito dell'incompletezza degli studi precedenti. Il campionamento entomologico è stato effettuato inizialmente su 20 stazioni, nove delle quali (Fig. 2) sono state successivamente studiate in modo più approfondito. Su otto di queste ultime (versanti del Monte Barro, tra le quote di 275 e 630 s.l.m.) è stato effettuato il rilevamento floristico, di proposito limitato all'analisi dei prati di versante.

Da un punto di vista fitoaltitudinale e vegetazionale il Monte Barro si sviluppa tra le fasce medioeuropea e subatlantica della regione medioeuropea (Pignatti, 1979), afferenti ai seguenti climax forestali potenziali: *Carpinion betuli* Issl. 31 em. Oberd. 57, *Tilio platyphylli-Acerion pseudoplatani* Klika 55 e *Quercion pubescenti-petraeae* Br.-Bl. 32 em. Rivas-Martinez 72. La realtà attuale presenta una situazione di notevole dinamismo vegetazionale, con esclusione delle aree rocciose, dove non esiste potenzialità forestale e il climax di base corrisponde alle formazioni casmofitiche dell'ordine *Potentilletalia caulescentis* Br.-Bl. in Br.-Bl. & Jenny 26. La parte sommitale del
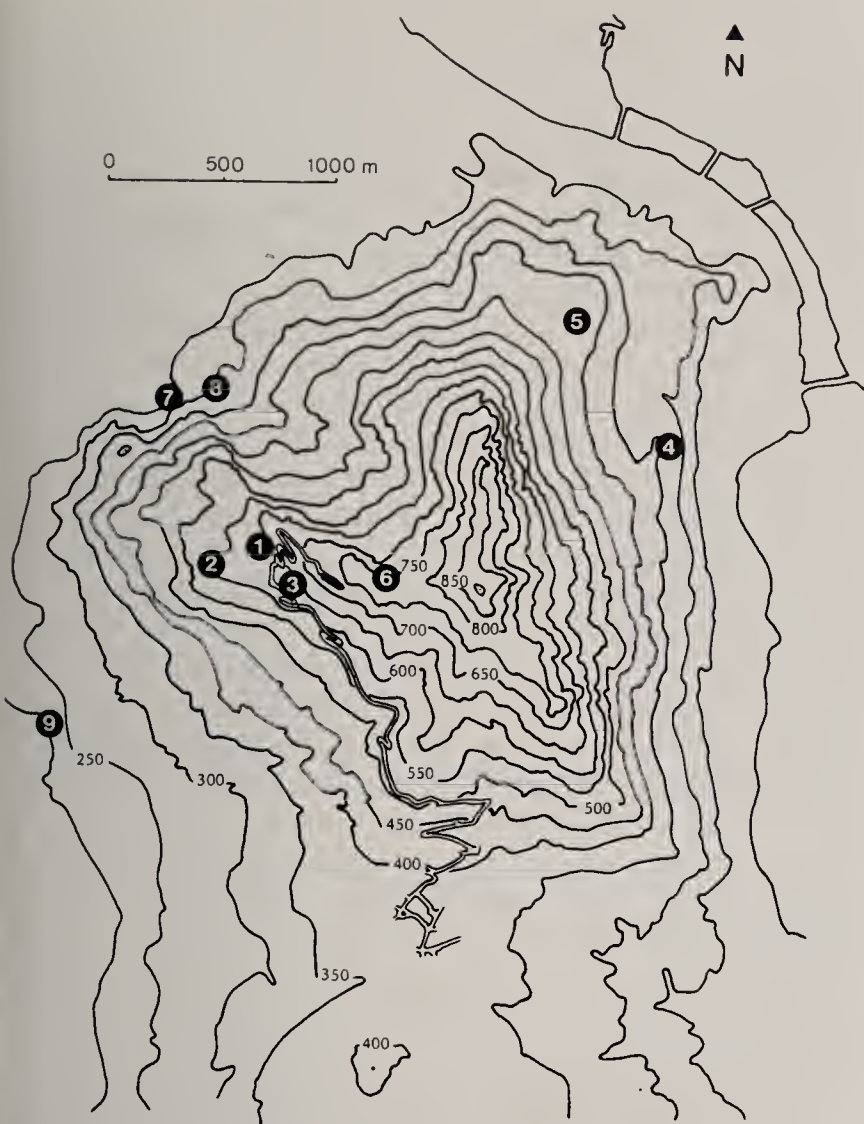
Fig. 2 - L'area campionata del Parco del Monte Barro. Sono indicati i numeri corrispondenti alle stazioni 1-9.

monte Barro, in corrispondenza del principale affioramento roccioso, concentra l'endemismo sudalpico, sudestalpico e insubrico. Ne sono esempi *Physoplexis comosa*, *Telekia speciosissima*, *Campanula raineri*, *Viola dubyana*, *Primula auricula* ecc. In numerose stazioni, per esempio a Pian Sciresa, la glacializzazione è stata totale e qui come altrove oggi si osserva un forte scollamento tra rizosfera e substrato pedogenetico, nel senso che la base calcarea smette precocemente di influenzare l'evoluzione del suolo a causa dell'intenso dilavamento, favorito anche dalle pendenze, un fenomeno comune e diffuso in tutta l'area insubrica. Qui la potenzialità vegetazionale è rappresentata da una brughiera riconducibile a formazioni dell'alleanza *Genistion* Böchh. 43, che vedono la partecipazione di *Calluna vulgaris*, *Genista germanica*, *Molinia caerulea* subsp. *arundinacea*, *Potentilla erecta*, *Stachys officinalis* e *Serratula tinctoria*. L'elemento arboreo in questo caso è rappresentato dal tremolo (*Populus tremula*) e dalla betulla (*Betula pendula*), molto frequenti in tutto il settore nordorientale del parco, la cui diffusione però sembra legata significativamente alla distribuzione degli incendi; questa pratica d'altra parte favorisce selettivamente la stessa brughiera.

La vegetazione attuale nell'ambito delle potenzialità forestali è il risultato di una fase generalizzata di abbandono e sospensione dell'attività umana sul suolo, al termine di una lunga storia di alterne vicende di contrazione ed espansione del bosco, determinate di volta in volta dai diversi momenti storico-economici. I versanti esposti a sud e a ovest, potenzialmente ricoperti di querceto termofilo a roverella, si caratterizzano oggi per una diffusione più o meno larga delle praterie a *Bromopsis erecta* (incl. *B. condensata*) e *Brachypodium rupestre* subsp. *caespitosum*. Queste possono essere riferite all'ordine *Brometalia erecti* Br.-Bl. 36 e a un'alleanza con carattere intermedio tra *Mesobromion erecti* Br.-Bl. & Moor 38 e *Diplachnion (Kengion)* Br.-Bl. 61, secondo il punto di vista di Royer (1991) che considera quest'ultimo syntaxon di posizione incerta tra i *Brometalia* e i *Festucetalia valesiacae* Br.-Bl. & Tx. 43. Gli aspetti più xerotermofili di dette praterie, particolarmente diffusi in corrispondenza degli affioramenti calcarei in buona esposizione, appartengono all'alleanza *Xerobromion* (Br.-Bl. & Moor 38) Moravec in Holub et al. 67; questo tipo di vegetazione non è stato preso in considerazione nel presente lavoro. Le praterie in generale denotano diversi gradi di inarbustamento in relazione alla tendenza autorigenerativa del bosco ora in atto. Specialmente i versanti orientali e settentrionali comprendono superfici a prato che ancora vengono in qualche modo gestite e che dal punto di vista fitosociologico corrispondono in media all'associazione *Centaureo dubiae (nigrescentis)-Arrhenatheretum elatioris* Oberd. 64. (Galasso 1994, ined.) Sia ai limiti del prato sia nel contesto delle praterie termofile, come pure nelle aperture del bosco, sono diffusissimi gli elementi di mantello, cioè associazioni del *Geranion sanguinei* Tx. 61 caratterizzate da elevate frequenze e coperture di *Geranium sanguineum, Origanum vulgare, Vincetoxicum hirundinaria, Knautia drymeia* subsp. *centrifrons*, *Teucrium chamaedrys* e *Thymus pulegioides*. La presenza di *Viola hirta, Potentilla alba* e *Trifolium medium* è facilitata dai processi locali di acidificazione del suolo e contrassegna una tipologia associazionale ascrivibile all'alleanza *Trifolion medii* Th. Müller 61. Infine merita un cenno la stazione di Ca' di Sala (Stazione 9 delle raccolte entomologiche), sulla riva settentrionale del bacino di Oggiono (lago di Annone), presa in considerazione nella ricerca entomologica come appendice del territorio del Monte Barro con caratteristiche ecologiche particolari. Qui la vegetazione non presenta regolare successione di cinture lungo un gradiente idrico a causa delle modificazioni geomorfologiche indotte dall'uomo; sono riconoscibili tre aspetti essenziali: 1) il canneto (*Phragmitetum australis* Schmale 39) con accenni di aggruppamento a *Iris pseudacorus*, elementi di magnocariceto (*Caricetum elatae* W. Koch 26) e residui di boscaglia ripariale (*Salicion cinereae* Müll. & Görs 58, *Alno-Ulmion* Br.-Bl. & Tx. 43); 2) il prato umido oligotrofico (*Molinion caeruleae* W. Koch 26); 3) vegetazione erbacea perenne e disorganizzata, al margine superiore della stazione, riconducibile alle classi *Artemisietea vulgaris* Lohm., Prsg. & Tx. in Tx. 50 (sottoclasse *Artemisienea vulgaris* Th. Müll. 81 in Oberd. 83) e *Plantaginetea majoris* Tx. 50 em. Oberd. et al. 67.

Benché necessaria, non è scopo della presente ricerca una verifica critica, in termini di moderne concezioni sistematiche e tassonomiche, della flora e della vegetazione del Monte Barro; per quanto sinora pubblicato si rinvia a Fornaciari (1994) e Cerabolini & Villa in Fornaciari (1994). Tuttavia lo studio botanico delle stazioni di rilevamento entomologico ha messo in evidenza aspetti, specialmente della flora, che inducono a prendere seriamente in considerazione il problema di una revisione globale, date le premesse numeriche (oltre un migliaio di specie secondo Fornaciari (1994)) e la particolare ricchezza di ambienti, per un'analisi delle biodiversità alfa e beta, davvero notevoli e ancora tutte da quantificare.

La flora delle stazioni rilevate: novità e precisazioni

Viene riportato qui di seguito, accompagnato da brevi note, l'elenco sistematico della flora delle otto stazioni oggetto del presente studio, precisando che il modello di ordinamento seguito, riguardo ai taxa di rango superiore al genere, è quello di Cronquist (1988) per quanto attiene le dicotiledoni e di Dahlgren (1989) per le monocotiledoni. Per semplicità i generi e le specie sono ordinati alfabeticamente all'interno delle famiglie. La nomenclatura binomia segue in linea di massima Pignatti (1982), tranne nei casi di aggiornamenti successivi derivati da specifici lavori di revisione sistematico-tassonomica e nomenclaturale, parte dei quali è riportata in Greuter et al. (1984-1991) e parte sarà citata all'occorrenza; in caso di discordanza nomenclaturale, il binomio usato in Flora d'Italia è riportato come sinonimo.

Pinaceae
Pinus sylvestris L. subsp. ***sylvestris***
Introdotta a scopo forestale, questa specie non sembra far parte del contesto vegetazionale attuale, almeno in termini climatici (isoepira alla vetta: 35°).

Aristolochiaceae
Aristolochia pallida Willd.

Ranunculaceae
Clematis recta L.
Helleborus niger L. subsp. ***niger***
Ranunculus acris L.
Ranunculus bulbosus L.
Thalictrum minus L.

Fagaceae
Quercus pubescens Willd.

Betulaceae
Corylus avellana L.
Ostrya carpinifolia Scop.

Caryophyllaceae
Cerastium fontanum Baumg. subsp. ***vulgare*** (Hartm.) Greuter & Burdet
(= *C. holosteoides* Fr. subsp. *triviale* (Spenn.) Möschl, non (Link) Möschl).
Petrorhagia saxifraga (L.) Link subsp. ***saxifraga***
Silene pratensis (Rafn) Godr.
(= *S. alba* (Mill.) Krause subsp. *alba*).
Per la nomenclatura si veda Aeschimann & Burdet (1994).
Silene vulgaris (Moench) Garcke subsp. ***vulgaris***

Polygonaceae
Rumex acetosa L.
Rumex acetosella L.

Clusiaceae
Hypericum perforatum L. subsp. ***perforatum***

Malvaceae
Malva alcea L.
La var. *fastigiata* (Cav.) Fiori, indicata da Fornaciari (1994) per questi popolamenti, non ha alcuna base sistematica rappresentando una delle tante combinazioni di stati di carattere (pelosità e incisioni della lamina) di natura tipicamente popolazionale, soggetta cioè a flusso genico continuo.

Cistaceae
Helianthemum nummularium (L.) Mill.
Fornaciari (1994) ritiene che i popolamenti in oggetto vadano attribuiti al tipo nominale della specie (subsp. *nummularium*), tuttavia, se il carattere riguardante la pagina inferiore della foglia (verde pallido, non bianco-grigiastro) è effettivamente in armonia con la descrizione originale del taxon, e ammesso che quest'ultimo sia consistente sul piano sistematico, l'entità in oggetto andrebbe riferita piuttosto alla subsp. *obscurum* (Celak.) Holub, che fra l'altro, secondo Pignatti (1982), sarebbe particolarmente frequente al piede delle Alpi. In ogni caso, sulla variabilità infraspecifica di *H. nummularium* vige ancora gran confusione, come si deduce dalla diversità delle trattazioni (cfr., per esempio, Flora d'Italia, Flora Europaea e Flora Iberica); sarà quindi opportuno, in attesa di una soddisfacente revisione, attenersi indicativamente al rango di specie.

Salicaceae
Populus tremula L.

Brassicaceae
Arabis collina Ten.
Biscutella laevigata L. subsp. ***laevigata***
Fornaciari (1994) identifica il popolamento barrense con la var. *glabra* Gaudin, della quale riconosce tre forme per altro assolutamente prive di valore, almeno finché non si disponga di un'adeguata interpretazione del modello di variabilità di questa specie.
Turritis glabra L.
(= *Arabis glabra* (L.) Bernh.).

Ericaceae
Calluna vulgaris (L.) Hull

Rosaceae
Amelanchier ovalis Medik. subsp. ***ovalis***
Cotoneaster nebrodensis (Guss.) Koch
Potentilla alba L.
Assieme a *Trifolium medium* e *Viola hirta* caratterizza la versione acidoclina della vegetazione di mantello, attribuibile all'alleanza *Trifolion medii* Th. Müller 61.
Potentilla recta L.
Fornaciari (1994) ne identifica la var. *obscura* (Nestl.) Koch nei «prati aridi a Coera», ma gli esemplari da noi rilevati nel prato sopra al Monumento dell'Alpino (ril. 3) presentano costantemente petali giallo sbiadito e corrispondono dunque al tipo nominale (var. *recta*). La convivenza territoriale delle due forme cromatiche fa ritenere che esse non abbiano alcuna consistenza sistematico-tassonomica, tanto più che sembrerebbero fondate sull'incapacità di un solo allele di codificare per uno dei pigmenti vacuolari dei petali.
Prunus avium L.
Sanguisorba minor Scop. subsp. ***minor***
Sorbus aria (L.) Crantz

Fabaceae
Anthyllis vulneraria L. subsp. ***weldeniana*** (Rchb.) Cullen provv.
(= *A. v.* subsp. *polyphylla* sensu Fornaciari et sub-

sp. *praepropera* sensu Fornaciari, *A. x adriatica* Beck sensu Pignatti).

La tassonomia di questo difficile pool di variazione infraspecifica (gruppo *maura* di Pignatti (1982)) è completamente in alto mare per la mancanza di un convincente riferimento sistematico. In altra occasione (Banfi, 1983) si ritenne di attribuire l'entità in oggetto al presunto notomorfo *A. x adriatica* Beck sensu Pignatti, epiteto comunque inadeguato perché oltre tutto di rango specifico, al quale sembrava meglio corrispondere la combinazione dei caratteri in uso osservati. Tuttavia sia il numero di segmenti delle foglie inferiori, sia la pelosità del calice, sia il pattern della pigmentazione (giallo e rosso variamente distribuiti su corolla e calice), si mostrano incostanti e imprevedibili fra segmenti contigui di popolazione. Fornaciari (1994) in questi popolamenti identifica senza ombra di dubbio le sottospecie *polyphylla* (DC.) Nyman e *praepropera* (A. Kern.) Bornm. (per non parlare delle «indispensabili» precisazioni sulle forme), assunto inaccettabile perché scientificamente privo di verifica. L'adozione da parte nostra del trinomio *A. vulneraria* subsp. *weldeniana*, in sintonia con Greuter et al. (1991), intende unicamente e provvisoriamente riportare sotto questa combinazione, comunque formalmente prioritaria rispetto ad *A. x adriatica*, tutta la variazione di tipo *maura* osservata nel territorio. Ciò in attesa di futuri chiarimenti sistematici e nomenclaturali.

Chamaecytisus hirsutus (L.) Link subsp. ***hirsutus***

La revisione di Cristofolini (1991) relativa a *Cytisus* sect. *Tubocytisus* ha indubbiamente portato nuova luce sulle affinità all'interno del gruppo. Tuttavia non ci sentiamo di condividere un'inclusione tout-court di *Chamaecytisus* Link in *Cytisus*, poiché nel complesso riteniamo continuino a sussistere chiari elementi morfosistematici di base, di notevole valore operativo, che rendono comunque *Chamaecytisus* una realtà congruente a livello di genere. Anche la recente monografia di Pajero et al. (1994) continua a mantenere separati i generi in questione.

Cytisophyllum sessilifolium (L.) O. Lang

(= *Cytisus sessilifolius* L.).

Nomenclatura secondo Greuter et al. (1991).

Cytisus emeriflorus Rchb.

Interessante endemita sudestalpico (non «insubrico» come altrove indicato, ma a corocentro insubrico) con una disgiunzione nelle Prealpi Friulane.

Cytisus scoparius (L.) Link

Genista germanica L.

Genista tinctoria L. subsp. ***tinctoria***

L'indicazione di Fornaciari (1994) della subsp. *ovata* (Waldst. & Kit.) Arcang. per i boschi tra l'Eremo e Pian Sciresa lascia notevoli perplessità in base a quanto sinora noto sulla corologia (Pignatti, 1982), ma soprattutto per la mancanza di studi moderni sulla variabilità infraspecifica. Certo, come esemplari di ambiente boschivo, è lecito sospettare trattarsi di semplice ecomorfosi.

Hippocrepis comosa L.

Lathyrus pratensis L.

Lotus corniculatus L.

Medicago lupulina L.

Ononis spinosa L. subsp. ***spinosa***

Trifolium campestre Schreb.

Trifolium medium L.

Per l'ecologia si veda quanto detto a proposito di *Potentilla alba*.

Trifolium montanum subsp. ***montanum***

Trifolium pratense L. subsp. ***pratense***

Trifolium repens L. subsp. ***repens***

Vicia dumetorum L.

Entità nuova per la flora del Monte Barro. È stata da noi raccolta lungo il margine boschivo del prato a nord del Monumento dell'Alpino (ril. 3). Galasso (1989/90, ined.) ne ha confermato di recente la presenza anche nel Triangolo Lariano (MSNM).

Vicia sativa L. subsp. ***nigra*** (L.) Ehrh.

(= *V. s.* subsp. *angustifolia* (Grufberg) Gaudin , *V. s.* subsp. *segetalis* (Thuill.) Gaudin).

Nomenclatura secondo Greuter et al. (1991).

Vicia sepium L.

Vicia villosa Roth subsp. ***villosa***

Santalaceae

Thesium bavarum Schrank

Euphorbiaceae

Euphorbia cyparissias L.

Frequenti clorosi, deformazioni e sterilità indotte da *Uromyces pisi* (Pers.) de Bary.

Euphorbia flavicoma DC. subsp. ***verrucosa*** (Fiori) Pignatti

Rhamnaceae

Rhamnus saxatilis Jacq.

Polygalaceae

Polygala vulgaris L.

Geraniaceae

Geranium nodosum L.

Geranium sanguineum L.

Apiaceae

Astrantia major L. subsp. ***major***

Cervaria rivinii Gaertn.

(= *Peucedanum cervaria* (L.) Lapeyr.).

Sistematica e nomenclatura secondo Pimenov & Leonov (1993).

Daucus carota L. subsp. ***carota***

Heracleum sphondylium L. subsp. ***sphondylium***

Oreoselinum nigrum Delarbre

(= *Peucedanum oreoselinum* Moench).

Sistematica e nomenclatura secondo Pimenov & Leonov (1993).

Pimpinella major (L.) Huds.

Trinia glauca (L.) Dumort.

Asclepiadaceae

Vincetoxicum hirundinaria Medik.

Convolvulaceae

Convolvulus arvensis L.

Boraginaceae

Echium vulgare L.

Lamiaceae

Clinopodium vulgare L.

Origanum vulgare L.

Prunella grandiflora (L.) Schöller

Salvia pratensis L.

Stachys alopecuros (L.) Benth. subsp. ***alopecuros***

Stachys officinalis (L.) Trevis. subsp. ***officinalis***

Stachys recta L. subsp. ***recta***

Teucrium chamaedrys L.
Teucrium montanum L.
Thymus pulegioides L.

Plantaginaceae
Plantago lanceolata L.
Plantago major L. subsp. ***major***

Oleaceae
Fraxinus ornus L.

Scrophulariaceae
Melampyrum cristatum L.
Rhinanthus alectorolophus (Scop.) Pollich
Verbascum thapsus L. subsp. ***thapsus***
Stranamente questa specie è passata inosservata nel territorio del Monte Barro. Convive con la congenere *V. lychnitis* L. non riportata nel presente elenco in quanto estranea ai rilievi, nel prato a nord del Monumento dell'Alpino (ril. 3), dove si presume sia comparsa sinantropicamente.
Veronica arvensis L.
Veronica chamaedrys L.

Globulariaceae
Globularia cordifolia L.
Globularia nudicaulis L.

Campanulaceae
Phyteuma scheuchzeri All. subsp. ***columnae*** (Gaudin) Bech.
Phyteuma spicatum L. subsp. ***spicatum***

Rubiaceae
Cruciata glabra (L.) Ehrend.
Galium album Mill.
Galium lucidum All.
Galium mollugo L.
Galium rubrum L.
Galium verum L. subsp. ***verum***

Adoxaceae
Viburnum lantana L.
Riguardo all'attribuzione di *Sambucus* e *Viburnum* alle Adoxaceae, qui adottata dagli scriventi, si veda Zomlefer (1994). I due generi, diversamente, possono essere considerati tipi di famiglie distinte (Sambucaceae, Viburnaceae), in ogni caso senza relazioni con le Caprifoliaceae (Bolli, 1994).

Valerianaceae
Valeriana collina Wallr.

Dipsacaceae
Knautia arvensis (L.) Coult.
Knautia drymeia Heuff. subsp. ***centrifrons*** (Borbás) Ehrend.
Knautia transalpina (H. Christ) Briq.
Knautia velutina Briq.

Asteraceae
Achillea collina Becker
La specie non compare nell'elenco floristico del Barro (Fornaciari, 1994). È entità subsinantropica, che predilige i siti marginali asciutti e ben esposti.
Achillea roseoalba Ehrend.
Anche questa entità non è riportata da Fornaciari (1994); probabilmente l'autore la identifica collettivamente con la precedente come *A. millefolium* L. Si tratta di specie propria dei prati mesofili, caratterizzante il centaureo-arrenatereto.
Bellis perennis L.
Buphthalmum salicifolium L. subsp. ***salicifolium***
La var. *grandiflorum* (L.) Fiori riportata da Fornaciari (1994) senza citazione del revisore è un'entità da interpretarsi, secondo Bechi & Garbari (1994), come parte di un «commiscuum» (Danser, 1929), cioè un insieme di individui interfecondi costituito da biotipi geografici eteromorfi (facies regionali) formatisi per selezione differenziale. Uno di questi biotipi è appunto la varietà in oggetto, che caratterizza la parte occidentale dell'areale della specie (dalle Alpi Marittime alle Retiche).
Centaurea grinensis Reut. subsp. ***grinensis***
Secondo Dostál (1976) questa entità è meritevole di rango specifico, tanto più comportando essa una vicariante geografica (subsp. *fritschii* (Hayek) Dostál), propria dei rilievi dell'Est europeo, che raggiunge le Alpi di striscio (Triestino, Friuli, Carnia (Pignatti, 1982)). Rispetto a *C. scabiosa* L., con cui convive nel territorio in studio, la nostra specie si distingue per le appendici delle squame non o poco decorrenti, con fimbrie brevi o assenti. Può considerarsi endemica sudestalpica.
Centaurea nigrescens Willd.
Questa specie, comunissima nei prati falciati, stranamente non compare nell'elenco di Fornaciari (1994).
Centaurea rhaetica Moritzi
Fornaciari (1994) alla vetta, in esposizione orientale, riconferma la presenza della var. *ensifolia* (Rota) Fiori (basionimo: *C. austriaca* Willd. var. *ensifolia* Rota) già indicata dallo stesso Fiori (1927) per il Monte Barro. Dal pool di variazione di *C. rhaetica* è stata recentemente separata *C. bugellensis* Soldano (Soldano, 1996), endemica del Biellese e della Val Sesia e in tale occasione lo stesso autore ha riesaminato anche il taxon di Rota confermando l'opportunità di mantenerne almeno per ora il rango varietale.
Centaurea triumfettii All. subsp. ***triumfettii***
Le due forme riportate da Fornaciari (1994), citate tra l'altro senza revisore, sono del tutto inconsistenti.
Erigeron annuus (L.) Pers.
Hieracium umbellatum L.
Inula hirta L.
Che cosa intende Fornaciari (1994) con «f. *policephala*» (sic!)?
Leontodon hispidus L. subsp. ***hispidus***
Leucanthemum vulgare Lam.
Scorzonera austriaca Willd.
Serratula tinctoria L. subsp. ***tinctoria***
Pignatti (1982) riporta due varietà, secondo Fornaciari (1994) entrambe presenti nel territorio del Barro. Tuttavia essendo grandissima e ancora quasi del tutto inesplorata la variabilità infraspecifica, come già facevano notare Cannon & Marshall (1976), preferiamo astenerci dal prendere posizione oltre la sottospecie.
Tanacetum corymbosum (L.) Sch. Bip. subsp. ***corymbosum***
Taraxacum sp. aggr. ***officinale***
Non siamo in grado di fornire precisazioni sull'identità di questo taxon, problema che richiederebbe un esame approfondito sulla variabilità di «*T. officinale* Weber» nell'intero territorio prealpino.
Tragopogon pratensis L. subsp. ***pratensis***

Convallariaceae
Polygonatum odoratum (Mill.) Druce
La «f. *angustifolia*» (sic!) proposta da Fornaciari (1994) per una «forma nemorosa a foglie strette» è priva di valore tanto sul piano formale (nomen nudum) come su quello della sostanza (variazione individuale occasionale).

Hyacinthaceae
Ornithogalum pyrenaicum L.

Liliaceae
Lilium bulbiferum L. subsp. ***croceum*** (Chaix) Baker

Orchidaceae
Gymnadenia conopsea (L.) R. Br.
Ophrys sphegodes Mill. subsp. ***sphegodes***
(non «sphecodes» come in Fornaciari (1994)).

Cyperaceae
Carex austroalpina Bech.

Poaceae
Anthoxanthum odoratum L.
Arrhenatherum elatius (L.) P. Beauv.
Brachypodium rupestre (Host) Roem. & Schult. subsp. ***caespitosum*** (Host) H. Scholz
Nonostante la revisione di Lucchese (1987) per le specie italiane e quella più recente di Schippmann (1991) per il genere *Brachypodium* in Europa, alle quali si rimanda per i dettagli, nei prospetti floristici si continua a leggere «*B. pinnatum* (L.) P. Beauv.» (tra questi Fornaciari, 1994), quando le uniche stazioni italiane di tale specie, finora note con certezza, sono localizzate nei settori più continentali delle Alpi. Il medesimo errore viene purtroppo ripreso in modo acritico anche nei lavori vegetazionali (nella fattispecie si veda Cerabolini & Villa in Fornaciari, 1994).
Briza media L.
Bromopsis erecta (Huds.) Fourr.
(= *Bromus erectus* Huds.).
L'elevazione a genere di *Bromus* L. sect. *Pnigma* Dumort. è in linea con il punto di vista -da noi condiviso- di diversi autori, a partire da Tzvelev (1976) per arrivare a Stace (1991). Il popolamento qui esaminato presenta occasionalmente individui con i caratteri di *B. condensata* (Hack.) Holub (guaine fogliari lanose e pannocchia contratta), il cui significato sistematico, nel caso di un'esatta corrispondenza tipologica, è tutto da discutere, come del resto è da discutere la congruenza delle altre variazioni del gruppo (*B. stenophylla, B. transsilvanica* ecc.), visto che oltre tutto non si differenziano per nulla sul piano ecologico.
Dactylis glomerata L. subsp. ***glomerata***
Festuca valesiaca Schleich.
La specie, abbastanza diffusa nei brometi della zona archeologica affacciati a sud, non è riportata da Fornaciari (1994). Come del resto non sono riportate altre entità dello stesso genere, piuttosto frequenti, che non possiamo includere nel presente elenco in quanto estranee ai rilievi, ma che riteniamo doveroso segnalare per la flora del Monte Barro. *F. stricta* Host subsp. *trachyphylla* (Hack.) Patzke (= *F. trachyphylla* (Hack.) Krajina, *F. brevipila* Tracey), già indicata da Ardissone (1903) sub «*F. duriuscula*», si incontra sui pendii soleggiati a sudovest del Monumento dell'Alpino; *F. rubra* L. subsp. *fallax* (Thuill.) Nyman (= *F. diffusa* Dumort., *F. heteromalla* Pourr., F. *rubra* L. subsp. *megastachys* Gaudin) è frequente in diversi punti a monte della strada per S. Michele, in direzione di Pian Sciresa.
Helictotrichon pubescens (Huds.) Pilger
(= *Avenula pubescens* (Huds.) Dumort.).
Entità nuova per la flora del Barro, in ogni caso piuttosto comune negli arrenatereti e stranamente passata inosservata.
Koeleria pyramidata (Lam.) Domin
Lolium perenne L.
Molinia caerulea L. subsp. ***arundinacea*** (Schrank) K. Richter
(= *M. arundinacea* Schrank, *M. c.* subsp. *a.* (Schrank) «Paul»).
Fornaciari (1994) di questa entità riferisce «Zone paludose...», indicazione che lascia molte perplessità poiché non corrisponde all'ecologia del taxon. D'altra parte l'autore sembra ignorare la grande diffusione di questa sottospecie sui versanti, specialmente settentrionale e orientale (compresa la brughiera di Pian Sciresa), in condizioni di umidità superficiale e lisciviazione evidenti. È nostra opinione che tutte le indicazioni relative a «*M. coerulea*» vadano invece riferite a questo taxon.
Poa pratensis L.
Schedonorus pratensis (Huds.) P. Beauv. subsp. ***pratensis***
(= *Festuca pratensis* Huds.).
L'adozione di un genere distinto in questo caso è in accordo con quanto espresso da Kerguélen & Plonka (1989) riguardo a *Festuca* s.l. e rappresenta la soluzione opposta a quella che propone Darbyshire (1993) – secondo noi assurdamente riduttiva – di trasferire al genere *Lolium* tutte le entità di *Festuca* subgen. *Schedonorus*.
S. arundinaceus (Schreb.) Dumort. subsp. *arundinaceus* (= *Festuca arundinacea* Schreb.) viene qui segnalata, anche se non compresa nei rilievi, in quanto comune e diffusa specialmente nel piano basale e, ancora una volta, inspiegabilmente non riportata nella Flora di Fornaciari (1994).
Sesleria caerulea (L.) Ardoino
(= *S. albicans* Kit., *S. varia* (Jacq.) Wettst., nom. superfl.).
Trisetaria flavescens (L.) Baumg. subsp. ***flavescens***
(= *Trisetum flavescens* (L.) P. Beauv.).
La specie non è molto comune e si concentra più che altro nei prati eutrofici. Per la tassonomia e la nomenclatura si veda Banfi & Soldano (1996).

Brevi considerazioni sulla vegetazione dell'area rilevata

I rilievi fitosociologici effettuati in corrispondenza delle stazioni di raccolta entomologica corrispondono a fasi aperte della vegetazione e, salvo il quinto (Pian Sciresa), appartengono tutti a potenzialità forestale. Agli effetti delle interrelazioni floro-faunistiche sembra utile un breve riepilogo degli elementi salienti. Nella tabella 1 per ogni rilievo vengono riportate 1) le specie con presenza >1, cioè non esclusive, che ricoprano più del 5% della superficie, 2) le specie con una sola presenza che caratterizzano in modo esclusivo la stazione. La tabella 1 non è ordinata fitosociologicamente, ma alfabeticamente per taxa, e i valori sono quelli di abbondanza-dominanza della scala di Braun-Blanquet trasformati secondo van der Maarel

(tabella di calcolo). Sebbene non evidenziati in apposito quadro d'associazione, si può arguire che i syntaxa meglio rappresentati sono: *Arrhenatheretalia* e *Arrhenatherion*, *Brometalia* e *Mesobromion/Diplachnion*, *Origanetalia*, *Quercetalia pubescenti-petraeae*, *Fagetalia* e *Carpinion*, e inoltre un manipoletto di specie pertinenti al *Genistion* che isolano il rilievo 5 (Pian Sciresa) dal contesto generale.

Tab. 1 - Elenco alfabetico delle specie con i valori di copertura secondo van der Maarel.

Rilievo n°	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Quota (m s.l.m.)	*610*	*600*	*630*	*325*	*435*	*750*	*275*	*305*
Inclinazione (°)	*5*	*5*	*8*	*20*	*5*	*30*	*5*	*5*
Esposizione	*W*	*W*	*W*	*E*	*NE*	*S*	*NW*	*NW*
Copertura (%)	*97*	*98*	*95*	*98*	*99*	*85*	*98*	*98*
Achillea collina	2	2	2	0	0	0	0	0
Achillea roseoalba	0	0	2	2	0	0	2	2
Amelanchier ovalis	0	0	0	0	0	2	0	0
Anthoxanthum odoratum	0	0	0	2	0	0	0	0
Anthyllis vulneraria weldeniana	2	0	0	2	0	2	0	0
Arabis collina	0	0	0	7	0	0	0	0
Aristolochia pallida	0	2	2	0	0	0	0	0
Arrhenatherum elatius	2	8	5	7	0	0	2	2
Astrantia major	0	0	0	0	0	0	0	3
Bellis perennis	2	0	0	0	0	0	0	0
Biscutella laevigata	0	0	0	2	2	0	0	0
Brachypodium rupestre caespitosum	0	0	0	0	8	0	0	8
Briza media	0	0	0	0	0	2	0	2
Bromopsis erecta	0	2	7	2	0	2	0	2
Buphthalmum salicifolium	0	0	0	0	0	0	0	2
Calluna vulgaris	0	0	0	0	5	0	0	0
Carex austroalpina	0	0	0	0	0	2	0	0
Centaurea grinensis	0	2	2	0	2	2	0	2
Centaurea nigrescens	5	0	3	0	0	0	2	2
Centaurea rhaetica	0	0	0	0	0	2	0	0
Centaurea triumfettii	0	2	2	2	2	2	0	0
Cerastium fontanum vulgare	2	0	0	0	0	0	0	0
Cervaria rivinii	0	2	0	0	0	0	0	0
Chamaecytisus hirsutus	0	0	0	0	2	0	0	0
Clematis recta	0	0	0	0	2	2	0	0
Clinopodium vulgare	0	0	2	2	0	0	0	0
Convolvulus arvensis	0	0	2	0	0	0	0	0
Corylus avellana	0	0	0	0	0	2	0	0
Cotoneaster nebrodensis	0	0	0	0	0	2	0	0
Cruciata glabra	2	0	2	0	0	0	0	2
Cytisophyllum sessilifolium	0	0	0	0	0	2	0	0
Cytisus emeriflorus	0	0	0	0	2	0	0	0
Cytisus scoparius	0	0	0	0	2	0	0	0
Dactylis glomerata	3	2	2	0	0	2	2	2
Daucus carota	0	0	0	2	0	0	0	0
Echium vulgare	0	0	0	2	0	0	0	0
Erigeron annuus	0	0	2	0	0	0	0	0
Euphorbia cyparissias	0	0	2	0	2	0	0	0
Euphorbia flavicoma verrucosa	0	0	0	0	0	2	0	0
Festuca valesiaca	2	3	2	2	0	0	0	0
Fraxinus ornus	0	0	0	0	0	2	0	0
Galium album	0	0	2	2	0	0	0	0
Galium lucidum	0	0	0	0	0	2	0	0
Galium mollugo	0	0	0	0	0	0	2	0
Galium rubrum	0	0	0	0	0	2	0	0
Galium verum	2	3	2	2	2	0	0	2
Genista germanica	0	0	0	0	2	0	0	0
Genista tinctoria	0	0	0	0	2	2	0	0
Geranium nodosum	0	0	0	0	0	0	0	2
Geranium sanguineum	0	7	0	2	2	2	0	0
Globularia cordifolia	0	0	0	0	0	2	0	0
Globularia nudicaulis	0	0	0	0	0	2	0	0
Gymnadenia conopsea	0	0	0	0	0	2	0	0
Helianthemum nummul. obscurum	2	0	0	0	0	2	0	0
Helictotrichon pubescens	0	7	0	7	0	0	0	0
Helleborus niger	0	0	0	0	0	2	0	0
Hypericum perforatum	0	0	0	2	0	0	0	0
Inula hirta	0	0	0	0	2	2	0	2
Knautia arvensis	2	0	0	0	0	0	2	0
Knautia drymeia centrifrons	0	0	2	2	0	0	0	2
Knautia transalpina	2	0	0	2	0	2	0	0
Knautia velutina	3	2	2	2	0	0	0	0
Koeleria pyramidata	0	0	0	0	0	2	0	0
Lathyrus pratensis	0	0	2	0	0	0	0	0
Leontodon hispidus	2	3	2	2	2	0	0	0
Leucanthemum vulgare	0	0	2	0	0	0	0	2
Lilium bulbiferum	0	2	0	0	0	2	0	0
Lolium perenne	7	0	0	0	0	0	0	0
Lotus corniculatus	0	2	0	0	0	2	2	2
Malva alcea	1	0	2	0	0	0	0	0
Medicago lupulina	0	0	0	2	0	0	2	0
Melampyrum cristatum	0	0	0	0	0	2	0	0
Molinia caerulea arundinacea	0	0	0	0	5	0	0	0
Ononis spinosa	0	0	0	0	0	0	0	2
Ophrys sphegodes	0	0	0	0	0	0	2	0
Oreoselinum nigrum	0	2	0	2	0	2	2	2
Origanum vulgare	0	0	0	0	0	2	0	0
Ornithogalum pyrenaicum	0	2	0	0	0	0	0	2
Ostrya carpinifolia	0	0	0	0	0	2	0	0
Petrorhagia saxifraga	0	0	0	2	0	0	0	0
Phyteuma scheuchzeri columnae	0	0	0	0	0	2	0	0
Phyteuma spicatum	0	0	0	0	0	0	0	2
Pimpinella major	0	2	2	0	0	0	2	2
Pinus sylvestris	0	0	0	0	1	0	0	0
Plantago lanceolata	2	0	0	0	0	0	2	2
Plantago major	2	0	0	0	0	0	0	0
Poa pratensis	2	0	2	0	0	0	0	0
Polygala vulgaris	0	0	0	0	0	0	0	2
Polygonatum odoratum	0	0	0	0	2	2	0	0
Populus tremula	0	0	0	0	5	2	0	0
Potentilla alba	0	0	0	0	2	2	0	0
Potentilla recta	0	0	2	0	0	0	0	0
Prunella grandiflora	0	0	0	0	0	2	0	0
Prunus avium	0	0	0	0	0	0	0	2
Quercus pubescens	0	0	0	0	0	2	0	0
Ranunculus acris	2	2	2	0	0	0	2	0
Ranunculus bulbosus	2	0	0	0	0	0	0	0
Rhamnus saxatilis	0	0	0	0	0	2	0	0
Rhinananthus alectorolophus	2	2	0	3	0	0	0	0
Rumex acetosa	0	2	2	2	0	0	2	0
Rumex acetosella	2	0	2	0	0	0	0	0
Salvia pratensis	2	2	3	0	0	0	2	2
Sanguisorba minor	2	2	2	2	0	0	0	0
Schedonorus pratensis	0	0	2	0	0	0	0	0

Rilievo n°	*1*	*2*	*3*	*4*	*5*	*6*	*7*	*8*
Quota (m s.l.m.)	*610*	*600*	*630*	*325*	*435*	*750*	*275*	*305*
Inclinazione (°)	*5*	*5*	*8*	*20*	*5*	*30*	*5*	*5*
Esposizione	*W*	*W*	*W*	*E*	*NE*	*S*	*NW*	*NW*
Copertura (%)	*97*	*98*	*95*	*98*	*99*	*85*	*98*	*98*
Scorzonera austriaca	0	0	0	0	0	2	0	0
Serratula tinctoria	0	0	0	0	0	2	0	0
Sesleria caerulea	0	0	0	0	0	2	0	0
Silene pratensis	0	2	2	0	0	0	2	0
Silene vulgaris	2	0	2	3	0	0	2	0
Sorbus aria	0	0	0	0	0	2	0	0
Stachys alopecuros	0	2	2	0	0	0	0	0
Stachys officinalis	0	0	0	0	0	2	0	0
Stachys recta	0	0	2	0	0	2	0	0
Tanacetum corymbosum	0	0	0	0	0	2	0	5
Taraxacum officinale aggr.	2	0	0	0	0	0	2	0
Teucrium chamaedrys	0	0	0	0	2	2	0	0
Teucrium montanum	0	0	0	0	0	2	0	0
Thalictrum minus	0	2	2	5	2	0	0	0
Thesium bavarum	0	2	0	0	2	2	0	0
Thymus pulegioides	0	0	0	0	2	2	0	0
Tragopogon pratensis	0	0	0	0	0	2	0	0
Trifolium campestre	2	0	2	0	0	0	0	0
Trifolium medium	0	0	0	0	0	0	0	2
Trifolium montanum	0	2	0	0	0	0	0	0
Trifolium pratense	2	0	2	0	0	0	2	0
Trifolium repens	3	0	2	0	0	0	2	0
Trinia glauca	0	0	0	0	0	2	0	0
Trisetaria flavescens	7	2	5	7	0	0	2	0
Turritis glabra	0	0	2	0	0	0	0	0
Valeriana collina	0	2	0	0	0	0	0	0
Verbascum thapsus	0	0	2	0	0	0	0	0
Veronica arvensis	2	0	2	0	0	0	0	0
Veronica chamaedrys	2	0	0	0	0	0	0	0
Viburnum lantana	0	0	0	0	0	2	0	0
Vicia dumetorum	0	0	2	0	0	0	0	0
Vicia sativa nigra	0	0	0	0	0	0	2	0
Vicia sepium	0	2	0	0	0	0	0	0
Vicia villosa	0	2	2	0	0	0	0	0
Vincetoxicum hirundinaria	0	2	0	2	2	2	1	2

Agli effetti delle relazioni tra entomofauna e vegetazione ci è sembrato interessante fornire qualche dato di carattere preliminare sulla fitodiversità cenotica in termini di α-diversità. In base a precedenti esperienze (Ferrari & Galanti 1972, Ferrari & Grandi 1974, Banfi 1979, Anzaldi & al. 1988, Pignatti & al. 1991), abbiamo preferito l'indice di Shannon-Weaver (log base 2) per un confronto delle stazioni rilevate. Tuttavia, come osservano Lambshead et al. (1983), il corretto impiego del parametro richiede una verifica delle curve di k-dominanza (Fig. 3): se queste si intersecano attorno alla metà del loro tragitto il confronto degli indici di diversità non può considerarsi attendibile. Nella tabella 2 vengono riassunti i confronti possibili, indicati con simbolo +.

Per ogni riga e per ogni colonna i quattro numeri riportati corrispondono rispettivamenrte al numero della stazione di campionamento, al numero delle specie presenti, all'indice di Shannon e alla evenness.

Come si può osservare, la stazione del rilievo 6 (pendio a monte del sentiero che dall'ex-sanatorio conduce alla vetta), benché più aperta delle altre (copertura dell'85%), floristicamente è la più diversificata, presentando i massimi di specie e di evenness, mentre il rilievo 4 (S. Michele, presso il sentiero per Pian Sciresa), al quart'ultimo posto come numero di specie, risulta il meno «disordinato» a causa delle preponderanti coperture di *Arabis collina, Arrhenatherum elatius, Helictotrichon pubescens* e *Trisetaria flavescens*. L'analisi delle componenti principali (PCA) mostra che le prime due componenti della variazione (Fig. 4) si identificano con il grado di termoxerofilia (asse 1) manifestato dai *Brometalia,* e il grado di ripresa vegetazionale o stato di abbandono (asse 2) evidenziato da *Origanetalia* e *Prunetalia.* I rapporti gerarchici di somiglianza fra le stazioni sono visibili nel dendrogramma di Fig. 5, che è stato calcolato (UPGMA) sulla matrice dei coefficienti di similitudine percentuale. Le stazioni 1 e 3 corrispondono al prato mesofilo insubrico classico (*Centaureo nigrescentis-Arrhenatheretum*), come pure le stazioni 2 e 4, che tuttavia risentono di abbandono per la maggiore
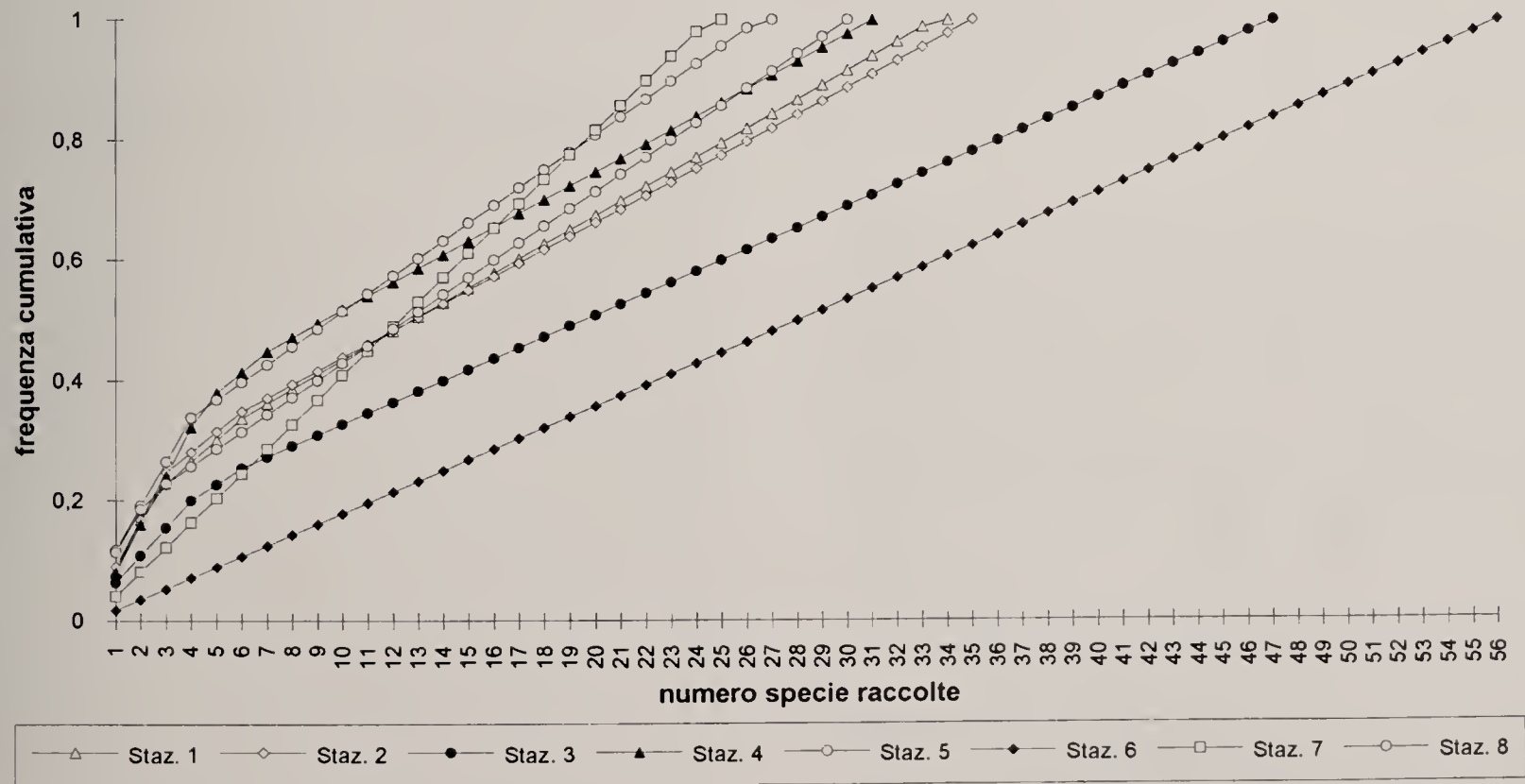
Fig. 3 - Curve di k-dominanza relative alle stazioni 1-8.

Tab. 2 - Confronto dei rilievi sulla base delle curve di k-dominanza. I quattro numeri delle caselle marginali indicano, dall'alto in basso: il numero di rilievo, il totale della specie, l'indice di diversità di Shannon e le evenness. Il simbolo + indica i confronti possibili.

	1 *34* *4,94* *0,97*	*2* *35* *4,95* *0,96*	*3* *47* *5,45* *0,98*	*4* *31* *4,74* *0,96*	*5* *27* *4,57* *0,96*	*6* *56* *5,81* *1*	*7* *25* *4,63* *0,99*
8 30 4,78 0,97	–	–	+	+	+	+	–
7 25 4,63 0,99	+	+	+	+	–	+	
6 56 5,81 1	+	+	+	+	+		
5 27 4,57 0,96	+	+	+	–			
4 31 4,74 0,96	–	–	–				
3 47 5,45 0,98	+	+					
2 35 4,95 0,96	–						

diffusione di elementi del *Geranion sanguinei/Trifolion medii*. In posizione intermedia, sotto quest'ultimo aspetto, si collocano le stazioni 7 e 8, che presentano in più una tendenza termoxerofila (*Mesobromion/Diplachnion*); infine le stazioni 5 e 6, pure in abbandono, identificano l'aspetto più termoxerofilo dell'area campionata con una preponderante presenza di elementi di *Brometalia, Mesobromion* e *Diplachnion*.

Caratteri specifici delle stazioni rilevate

Stazione 1: Località Piani di Barra, 610 m, esp. W, dal 1990 interessata da scavi archeologici in rapporto al cosiddetto Grande Edificio. Consistente presenza di prato falciabile che indica una attività di foraggio residua, testimoniata anche dalla non significatività del mantello.

Dominanze: *Lolium perenne, Dactylis glomerata, Centaurea nigrescens, Trisetaria flavescens, Knautia velutina, Trifolium repens.* Specificità: *Lolium perenne, Cerastium fontanum vulgare.*

Stazione 2: Località Piani di Barra, 600 m, esp. W, dal 1990 interessata da scavi archeologici in rapporto al cosiddetto Edificio II. Leggera prevalenza di prateria e mantello su prato falciabile, cioè netta risposta all'abbandono di una gestione a foraggio già indebolita.

Dominanze: *Galium verum, Geranium sanguineum, Arrhenatherum elatius, Festuca valesiaca, Leontodon hispidus, Helictotrichon pubescens.* Specificità: *Valeriana collina, Vicia sepium.*

Stazione 3: Conca prativa a monte del Monumento all'Alpino, 630 m, esp. W. Convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Dominanze: *Bromopsis erecta, Arrhenatherum elatius, Centaurea nigrescens, Salvia pratensis, Trisetaria flavescens.* Specificità: *Erigeron annuus, Potentilla recta, Convolvulus arversis, Turritis glabra, Verbascum thapsus, Schedonorus pratensis, Vicia dumetorum.*

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion erecti* (*Thalictrum minus, Arabis collina*) è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.
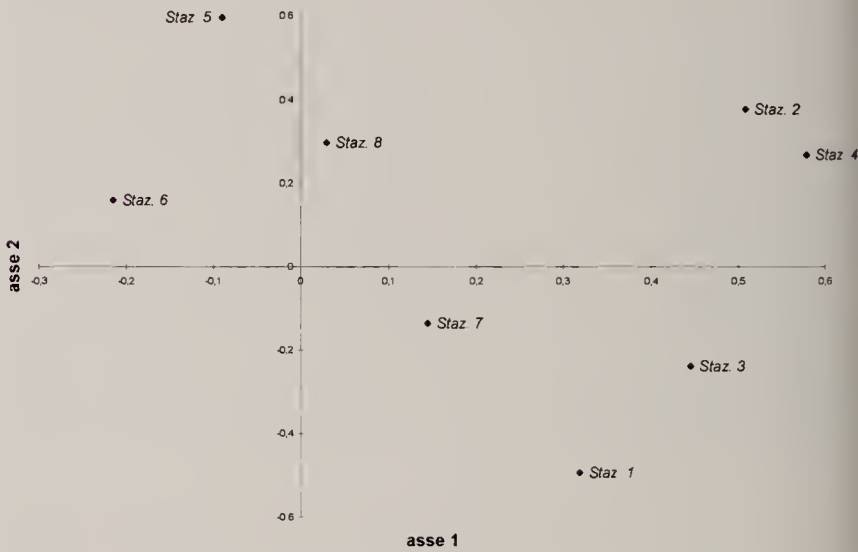
Fig. 4 - Confronto delle stazioni 1-8 mediante analisi delle componenti principali.
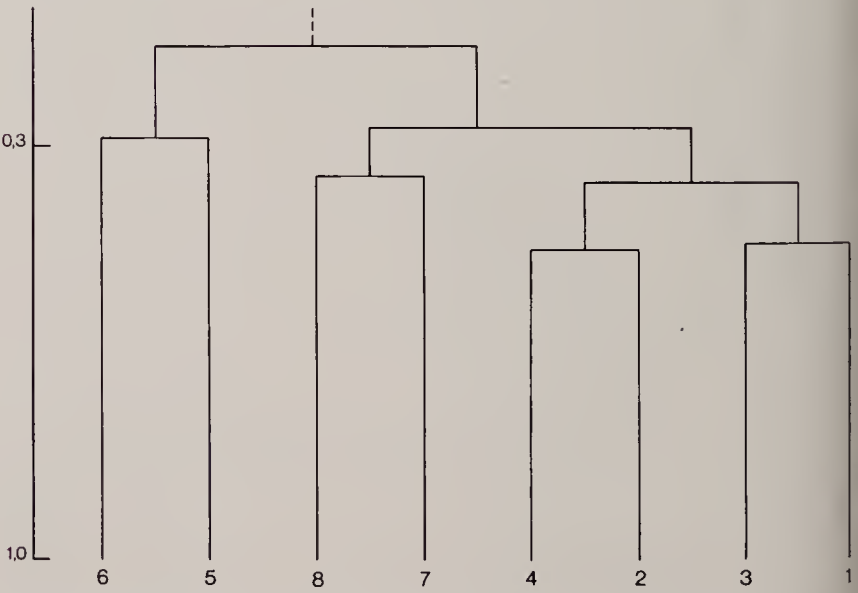
Fig. 5 - Dendrogramma delle stazioni 1-8 (WPGMA su Percent Similarity).

Dominanze: *Arrhenatherum elatius, Thalictrum minus, Silene vulgaris, Trisetaria flavescens, Rhinanthus alectorolophus, Arabis collina, Helictotrichon pubescens.* Specificità: *Petrorhagia saxifraga.*

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. Prato arido con montarozzi residuali a brughiera. Si caratterizza meglio di tutte le altre stazioni per la presenza dell'elemento di brughiera, accompagnato da *Cytisus emeriflorus*, endemismo calcicolo SE-alpico. Per il resto il livello di base è costituito da prateria a *Brachypodium rupestre caespitosum.*

Dominanze: *Brachypodium rupestre caespitosum, Calluna vulgaris, Molinia caerulea arundinacea, Populus tremula.* Specificità: *Calluna vulgaris, Chamaecytisus hirsutus, Cytisus emeriflorus, Cytisus scoparius, Genista germanica, Molinia caerulea arundinacea, Pinus sylvestris.*

Stazione 6: Superfici prative lungo il sentiero della «Cresta occidentale», che dall'edificio dell'ex sanatorio sale alla vetta, 750 m, esp. S. Prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura. Forte influsso dell'elemento prenemorale, con tendenza a un *Quescetum pubescentis* s. l. L'elemento di mantello ha scarso peso.

Dominanze: nessuna. Specificità: *Serratula tinctoria, Sorbus aria, Cytisophyllum sessilifolium, Helleborus niger, Cotoneaster nebrodensis, Globularia nudicaulis, Phyteuma scheuchzeri columnae, Centaurea rhaetica, Euphorbia flavicoma verrucosa, Carex austroalpina, Origanum vulgare, Gymnadenia conopsea, Amelanchier ovalis, Galium lucidum, Melampyrum cristatum.*

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè. Superficie prativa terrazzata all'interno del bosco mesofilo, 275 m, esp. NW. Molto simile a quella della stazione 8, ma più aperta e con qualche elemento in più di *Mesobromion.*

Dominanze: Nessuna. Specificità: *Ophrys sphegodes, Vicia sativa nigra.*

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè. Superficie prativa terrazzata all'interno del bosco mesofilo, 305 m, esp. NW. Prato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili. Ciò è conseguenza dell'esposizione fresca e di un maggiore sviluppo di suolo. Sono comunque sempre presenti gli elementi di prateria.

Dominanze: *Brachypodium rupestre caespitosum, Tanacetum corymbosum, Astrantia major.* Specificità: *Astrantia major, Prunus avium, Geranium nodosum.*

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Questa stazione non è stata rilevata fitosociologicamente, ma solo floristicamente. Vi si evidenziano tre aspetti essenziali: 1) il canneto (*Phragmitetum australis*) con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto (*Caricetum elatae*) e residui di boscaglia ripariale (*Salicion cinereae*); 2) il prato umido oligotrofico (*Molinion caeruleae*); 3) vegetazione erbacea perenne e disorganizzata, al margine superiore della stazione, riconducibile alle classi *Artemisietea vulgaris* e *Plantaginetea majoris.*

Fig. 6 - Facies marginale di prato mesofilo (*Centaureo nigrescentis-Arrhenatheretum*) con dominanza locale di *Helictotrichon pubescens* e *Rhinanthus alectorolophus*.

Fig. 7 - La brughiera di Pian Sciresa fisionomizzata da *Calluna vulgaris* e *Molinia caerulea* subsp. *arundinacea*.

Fig. 8 - *Bromopsis erecta* (incl. *B. condensata*), elemento caratterizzante il prato meso-xerofilo (*Mesobromion*).

Fig. 9 - *Anthyllis vulneraria* subsp. *weldeniana* provv., componente del *Mesobromion*, non è ancora risolta sul piano sistematico-tassonomico e presenta variabilità intrapopolazionale anche nella colorazione del calice e della corolla.

Fig. 10 - *Cotinus coggygria*, differenziale calcicola e termofila dell'ordine *Quercetalia pubescenti-petraeae*.

Fig. 11 - *Potentilla recta* var. *recta* nel prato sopra il monumento dell'Alpino (staz. 3).

Fig. 12 - *Festuca valesiaca* appartiene al contingente più continentale e caratterizza localmente il *Mesobromion* e lo *Xerobromion*.

Fig. 13 - *Stipa eriocaulis* subsp. *eriocaulis* caratterizza gli aspetti più xerotermofili, riscontrabili in affioramento calcareo (*Xerobromion*).

Fig. 14 - *Trinia glauca*, componente di *Xerobromion* e differenziale edafica (calcare).

Fig. 15 - *Thesium bavarum* è entità legata essenzialmente ai querceti di roverella su base calcarea.

Fig. 16 - *Clinopodium vulgare* fa parte del manipolo di specie guida della vegetazione di mantello (*Origanetalia*).

Fig. 17 - *Potentilla alba* differenzia in senso acidofilo e oligotrofico la vegetazione di mantello (*Trifolion medii*).

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Carlo Leonardi

Ricerca entomofaunistica nel parco regionale del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Si descrivono in modo sintetico i risultati di raccolte entomofaunistiche condotte nell'area del Monte Barro (Lecco) negli anni 1989-1992 dal Museo Civico di Storia Naturale di Milano. La ricerca è stata prevalentemente orientata al censimento dell'entomofauna fitofaga di stazioni prative. Sono state identificate 714 entità sistematiche appartenenti a Eterotteri, Coleotteri, Imenotteri, Sinfiti e Ragni; 65 taxa sono risultati nuovi per la Lombardia e 5 nuovi per l'Italia.

Abstract - Entomofaunistic researches in the regional park of Monte Barro (Italy, Lombardy, Lecco).
The results of a study carried out by the Natural History Museum of Milano in the area of Monte Barro (Lecco) during the years 1989-1992 are synthetically reported. Phytophagous species of meadows have been mainly collected: 714 taxa belonging to Heteroptera, Coleoptera, Hymenoptera of suborder Symphyta and spiders were identified; out of them, 65 proved new to Lombardy, 5 new to Italy.

Key words: entomology, faunistics, Monte Barro.

L'indagine che il Museo di Storia Naturale di Milano, col contributo del Consorzio Parco Monte Barro, ha condotto nell'area del Monte Barro durante gli anni 1989-1992 è stata prevalentemente orientata al censimento di insetti fitofagi o comunque catturabili coi sistemi in uso per la raccolta dell'entomofauna fitofaga. Sono stati studiati gli Eterotteri, alcune famiglie di Coleotteri (Elateridi, Coccinellidi, Crisomelidi, Cerambicidi, Curculionidi), gli Imenotteri Sinfiti e i Ragni, con un numero complessivo di 718 entità sistematiche, che risulta assai rilevante se si considera che il Monte Barro è un rilievo molto modesto, privo di specie strettamente orofile. Notevole è anche la segnalazione di ben 65 specie nuove per la Lombardia e, nel caso dei Ragni, di 5 specie nuove per la fauna italiana (v. Tabella 1).

Tabella 1 - Prospetto numerico delle specie raccolte (n= n° di specie; L= specie nuove per la Lombardia; I= specie nuove per l'Italia; %= percentuale di specie raccolte rispetto a quelle note per l'Italia).

	n	L	I	%
Heteroptera	169	13		12,03
Elateridae	27			11,49
Coccinellidae	23			18,10
Chrysomelidae	152	8		18,70
Cerambycidae	27	1		9,93
Curculionidae	166	9		8,71
Symphyta	43	2		7,26
Araneae	111	32	5	7,89
Totale	718	65	5	

Le raccolte sono state effettuate prevalentemente in 8 stazioni prative (staz. 1-8) all'interno del parco e in una stazione (staz. 9) esterna, situata sulla riva settentrionale del bacino di Oggiono del Lago di Annone, in località Ca' si Sala.

Durante tutto il periodo delle raccolte è stata utilizzata per le stazioni 1-9 una numerazione differente, che riteniamo opportuno indicare in quanto non è stata modificata sulle etichette che accompagnano gli esemplari: 1 (4b), 2 (4), 3 (3), 4 (9), 5 (1 e 1bis), 6 (8), 7 (18), 8 (16), 9 (6).

Per una descrizione delle singole stazioni si rimanda ai lavori di Banfi, Galasso & Sassi e Leonardi & Sassi in questo stesso volume. Tali descrizioni si riferiscono agli anni in cui sono state effettuate le raccolte.

Occorre infatti far presente che, essendo diventate più irregolari le tradizionali attività dell'economia agro-silvo-pastorale che consentivano il mantenimento delle cenosi erbacee, l'ambiente indagato risulta oggi ampiamente caratterizzato da un dinamismo verso la ricostruzione della foresta, quindi le variazioni che si osservano nei prati, quantomeno sotto il profilo fisionomico, possono essere rapidissime, con conseguenze sulla composizione dell'entomofauna. Il recupero totale della foresta, con conseguente scomparsa dei prati, causerebbe sicuramente un impoverimento faunistico.

Complessivamente sono state effettuate, da personale o da collaboratori del museo, 86 uscite giornaliere con un totale di 202 sopralluoghi di circa un'ora e mezza ciascuno nelle stazioni 1-9, ripartiti come in tabella 2.

Tabella 2 - Numero di sopralluoghi effettuati nei differenti mesi dell'anno nelle stazioni 1-9.

stazioni	1	2	3	4	5	6	7	8	9
marzo		1	1	2	1			1	3
aprile		2	2	1	3	1	2	2	5
maggio	3	8	7	6	7	6	3	5	13
giugno	4	10	4	9	7	2	1	1	5
luglio	1	2	2	4	5	6	2	3	3
agosto		3	1			1	1	2	1
settembre		3	2	4	2	4	2	2	2
ottobre	2	2	3	2	3	1			2
novembre									1
Totale	11	31	22	28	28	21	11	16	35

A queste uscite ne vanno aggiunte poche altre effettuate da due studentesse nell'ambito delle loro tesi di laurea sui Ragni e sui Curculionidi del Monte Barro.

Il numero di specie raccolto nelle singole stazioni per ognuno dei gruppi studiati è riportato nella tabella 3.

Tabella 3 - Prospetto numerico delle specie raccolte nelle stazioni 1-9.

stazioni	1	2	3	4	5	6	7	8	9
Heteroptera	64	74	56	82	59	32	29	34	40
Elateridae	6	13	8	9	6	7	2	3	6
Coccinellidae	10	9	13	12	10	7	3	6	15
Chrysomelidae	40	65	56	61	46	51	32	50	59
Cerambycidae	3	9	4	6	2	5	3	7	2
Curculionidae	49	82	60	44	73	48	39	29	40
Symphyta	10	13	5	11	5	8	5	5	10
Araneae	6	50	28	10	65	35	13	8	31
Totale	188	315	230	235	266	193	126	142	203

L'area più ricca di specie, per quanto riguarda il complesso dei gruppi studiati, sembra essere quella che comprende la stazione 2, in località Piani di Barra, interessata da scavi archeologici. Altre stazioni di rilievo per l'elevato numero di specie che vi è stato censito sono la staz. 3 (conca prativa a monte del monumento dell'Alpino, assai vicina in linea d'aria alle stazioni 1 e 2), la staz. 4 (prato falciabile in località San Michele) e la staz. 5 (in località Pian Sciresa), mentre sembrano relativamente poveri i prati della val Faè (stazz. 7 e 8). È ovvio tuttavia che il numero di specie censite nelle singole stazioni fornisce di per sè un'informazione modesta se non lo si collega al numero di uscite effettuate e soprattutto, ove possibile, all'andamento dei diagrammi di saturazione; questi ultimi sono stati costruiti solo per i Crisomelidi (v. Leonardi & Sassi: p. 191, Fig 2), in considerazione del fatto che a questo gruppo è stata rivolta una maggiore attenzione durante le raccolte.

La descrizione di una comunità semplicemente in termini di numero di specie presenti fa trascurare completamente un aspetto importante della sua struttura numerica, cioè la diversità. Alcune misure di diversità (indice di Shannon, evenness, curve di k-dominanza) sono state ricavate per i Crisomelidi (v. Leonardi & Sassi: pp. XX, Figg. 4, 5).

È infine interessante confrontare le stazioni 1-8 in base alle specie fitofaghe che vi sono presenti. Partendo da una matrice binaria (Tab. 4) in cui sono riassunti i dati relativi ai tre gruppi (Heteroptera, Curculionidae, Chrysomelidae) più importanti e meglio raccolti, si ricava, utilizzando l'indice di Dice/Sorensen e applicando la cluster analysis secondo il metodo WPGMA, il dendrogramma di somiglianza riportato in Fig. 1. In questo dendrogramma si nota l'isolamento delle stazioni 7-8 che corrispondono a due prati falciabili della Val Faè e, fra le rimanenti, la separazione della stazione 6, fisionomicamente ben caratterizzata dall'evidente discontinuità della copertura erbacea, che indica una forte ripresa del bosco.

Dal punto di vista zoogeografico l'entomofauna del Monte Barro, che presenta una tipologia climatica di tipo insubrico, sembra essere caratterizzata da una netta dominanza di taxa ad ampia distribuzione, da una presenza importante di elementi europei e da una scarsissima componente mediterranea, come si vede nella Fig. 2 dove sono posti a confronto i gruppi studiati raggruppando i corotipi per categorie sintetiche (Vigna Taglianti et al., 1991).
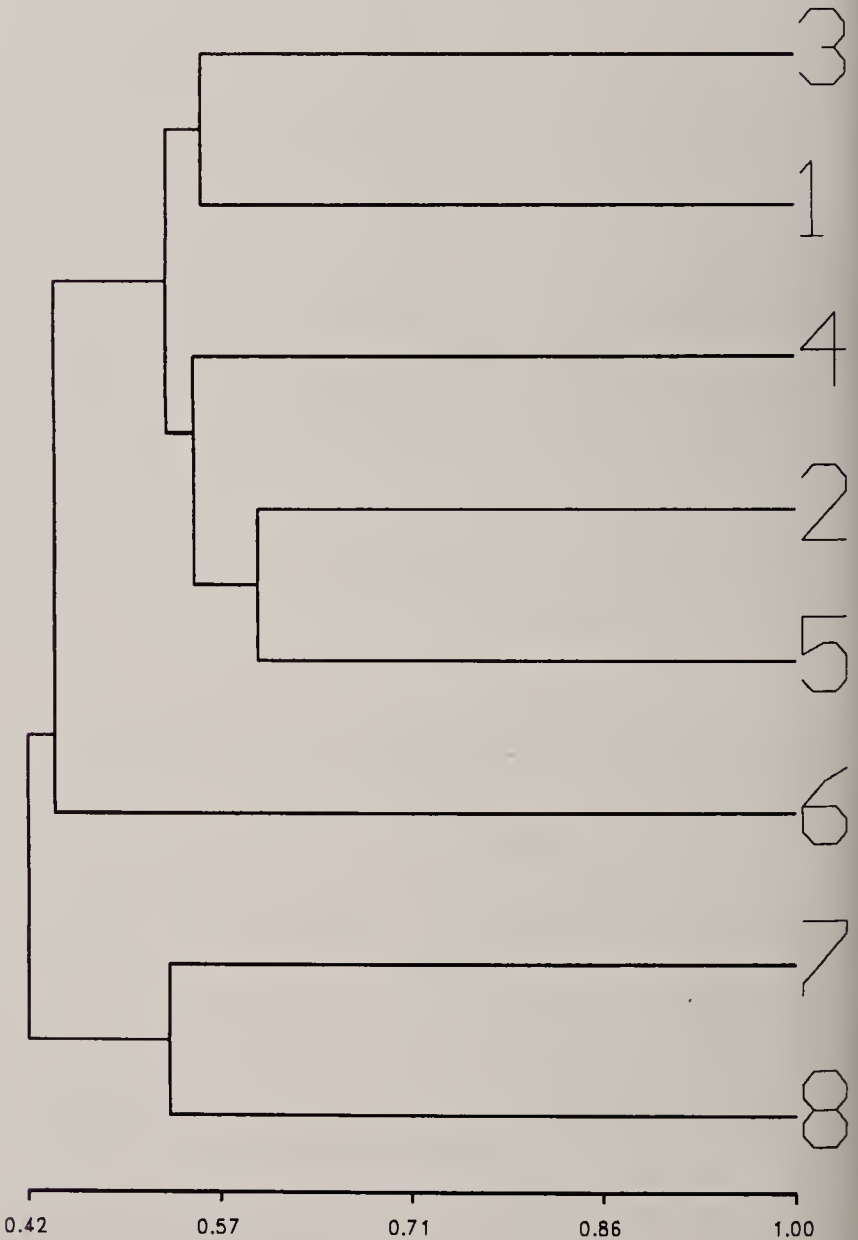
Fig. 1 - Dendrogramma di somiglianza delle stazioni 1-8 (indice di Dice/Sorensen + WPGMA).
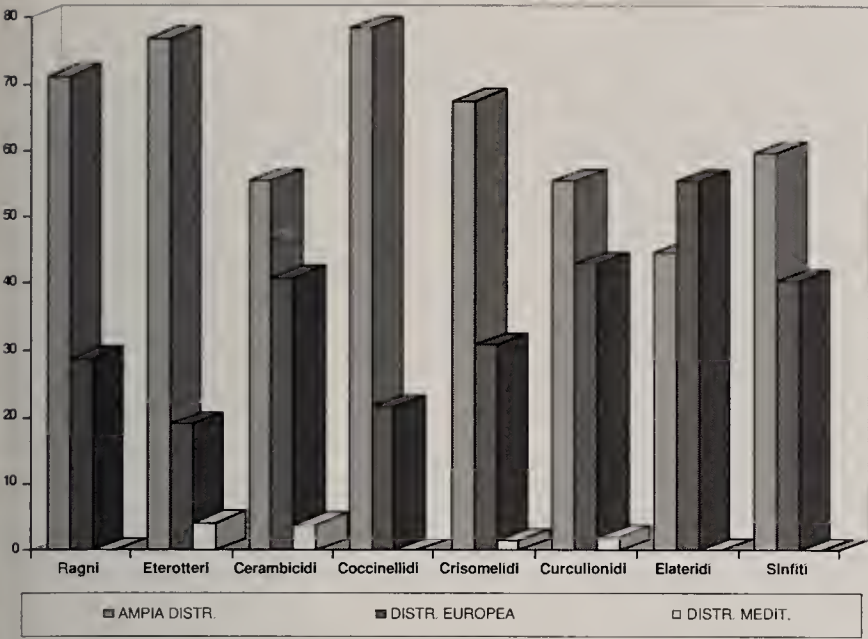
Fig. 2 - Spettro corologico nei gruppi studiati, con evidenziazione di tre categorie sintetiche: elementi ad ampia distribuzione paleartica, elementi a distribuzione europea, elementi a distribuzione mediterranea.

Complessivamente gli elementi ad ampia distribuzione (per lo più asiatico-europei, sibirico-europei o turanico-europei) sono circa il 66% e quelli a distribuzione europea (comprendendovi anche i pochi endemiti della fauna italiana) poco più del 30%, mentre la componente mediterranea corrisponde a meno del 2% delle specie raccolte (Fig. 3).
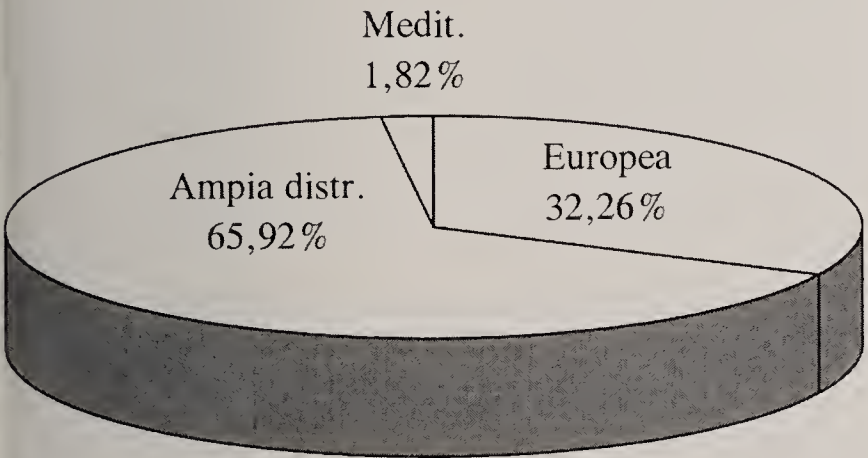
Fig.3 - Corotipi dei taxa raccolti sul Monte Barro raggruppati per categorie sintetiche.

Tabella 4 - Matrice binaria formata da 395 specie di Heteroptera (sono state escluse le specie predatrici), Chrysomelidae e Curculionidae raccolti nelle stazioni 1-8.

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Heteroptera								
Acanthosoma haemorrhoidale	0	1	0	0	0	0	0	0
Acompus rufipes	0	1	0	0	0	0	0	0
Adelphocoris lineolatus	0	1	1	1	1	0	1	1
Adelphocoris seticornis	1	1	1	0	0	0	0	1
Adelphocoris vandalicus	0	0	0	0	1	0	0	0
Aelia acuminata	1	1	0	1	0	0	0	0
Aellopus atratus	0	1	0	0	0	0	0	0
Alydus calcaratus	1	0	1	1	1	0	0	1
Beosus maritimus	0	1	1	1	0	0	0	0
Berytinus clavipes	0	0	0	1	1	0	0	0
Berytinus minor	0	0	0	1	0	0	0	1
Bryocoris pteridis	0	0	0	0	0	1	0	0
Calocoris striatellus	0	0	1	0	1	1	0	0

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Capsus ater	1	0	1	0	1	0	0	0
Carpocoris pudicus	0	1	1	0	1	1	1	1
Catoplatus fabricii	0	0	1	0	0	0	0	0
Charagochilus gyllenhali	1	1	1	1	0	1	1	1
Charagochilus weberi	0	0	1	0	0	1	0	0
Chlamidatus pulicarius	1	1	1	1	0	0	1	0
Copium flavicorne	1	1	0	1	1	1	0	1
Coptosoma scutellatum	0	1	1	1	0	1	0	0
Coreus marginatus	1	1	0	0	0	0	1	1
Coriomeris denticulatus	1	0	1	1	0	0	0	0
Coriomeris scabricornis	0	0	1	1	0	0	0	0
Corizus hyoscyami	0	1	1	1	0	0	1	1
Criocoris crassicornis	0	1	0	1	0	0	0	0
Cyllecoris histrionicus	1	0	0	0	0	0	0	0
Cymus aurescens	0	0	0	0	0	1	0	0
Dictyla echii	0	1	0	0	0	0	0	0
Dictyonota strichnocera	0	1	0	0	0	0	0	0
Dicyphus annulatus	0	0	0	0	1	0	0	0
Dicyphus flavoviridis	1	0	1	0	0	0	0	0
Dicyphus globulifer	1	0	1	0	0	0	0	0
Dolycoris baccarum	1	1	1	1	1	0	1	1
Driophylocoris flavoquadrimaculatus	1	1	1	0	0	1	0	0
Drymus ryeii	0	1	0	0	0	0	0	0
Drymus sylvaticus	1	1	0	1	0	0	0	1
Dryocoris sphacelatus	0	1	0	1	0	0	0	0
Dryocoris vernalis	0	1	0	1	1	0	1	0
Emblethis verbasci	1	1	0	0	0	0	1	0
Enoplops scapha	1	1	0	0	1	1	0	0
Eurigaster maurus	1	1	1	1	1	0	0	0
Eurigaster testudinarius	1	0	0	0	1	0	1	1
Eurydema oleraceum	1	1	1	1	1	0	1	1
Eurydema ornatum	0	0	0	1	0	0	0	0
Eurydema ventrale	0	0	0	1	0	0	0	0
Exolygus pratensis	1	1	1	1	0	0	0	1
Eysarcoris aeneus	0	1	0	0	1	0	0	0
Geocoris megacephalus	1	0	0	0	0	0	0	0
Globiceps horvathi	0	0	1	0	1	1	0	0
Globiceps shaegiformis	0	1	0	1	0	0	0	0
Gonocerus acuteangulatus	0	1	0	0	0	1	0	0
Graphosoma lineatum	0	1	0	1	0	0	0	0
Halticus apterus	1	0	1	1	1	0	0	1
Harpocera thoracica	1	0	1	0	0	1	0	0
Heterocordilus genistae	0	1	0	1	1	1	0	0
Heterocordilus tumidicornis	0	0	0	0	0	0	0	1
Heterogaster cathariae	1	0	0	0	0	0	0	0
Ischnodemus quadratus	0	1	0	0	0	0	0	0
Kalama tricornis	1	0	1	0	1	0	0	1
Kleidoceris resedae	1	1	0	1	1	0	0	0
Lasiacantha capucina	0	0	0	1	0	0	0	0
Legnotus limbosus	0	1	1	1	0	0	0	0
Legnotus picipes	0	0	0	1	0	0	0	0
Liocoris tripustulatus	0	0	1	1	1	0	0	0
Lygaeus equestris	1	1	1	0	1	1	0	0
Lygaeus saxatilis	0	0	0	1	0	0	0	0
Macroplax fasciatus fasciatus	1	0	0	0	1	0	1	0
Macroplax preyssleri	1	1	0	1	1	1	0	1
Megaloceroea recticornis	0	1	0	1	1	0	0	0
Megalonotus antennatus	0	0	0	0	0	0	0	1
Megalonotus dilatatus	0	0	0	0	1	0	0	0
Megalonotus praetextatus	1	0	0	0	0	0	0	0
Nezara viridula	0	0	0	0	0	0	1	0
Notostira erratica	0	0	1	1	0	0	0	1
Nysius ericae	0	0	0	1	0	0	0	0
Nysius senecionis	1	0	0	1	0	1	0	0
Nysius thymi	0	0	0	1	0	0	0	0
Odontotarsus purpureolineatus	0	1	0	0	0	1	0	0
Onchochila simplex	0	0	0	1	1	0	0	0
Pinalitus atomarius	0	0	0	1	0	0	0	0
Orthops kalmi	0	1	1	0	1	1	0	0
Oxycarenus pallens	1	1	0	0	1	1	0	0

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Palomena prasina	0	1	0	0	1	0	0	0
Pantilius tunicatus	0	1	0	1	0	0	0	0
Paromius leptopoides	1	0	0	0	1	0	0	0
Pentatoma rufipes	1	1	0	0	0	0	0	0
Peritrechus geniculatus	1	0	1	1	1	0	1	0
Peritrechus gracilicornis	1	0	1	1	1	0	1	0
Phylus coryli	0	0	0	1	0	0	0	0
Piezodorus lituratus	1	1	0	0	1	1	1	0
Platyplax salviae	1	0	1	1	0	0	1	0
Plinthisus brevipennis	0	0	0	1	0	0	0	0
Podops inuncta	1	1	0	0	1	0	0	0
Polymerus unifasciatus	0	1	1	1	1	1	0	1
Psallus variabilis	1	0	0	1	1	0	0	0
Pyrrhocoris apterus	1	0	1	0	0	0	0	0
Rhopalus conspersus	0	1	1	1	1	1	1	0
Rhopalus parumpunctatus	1	1	1	1	0	0	0	0
Rhopalus subrufus	1	1	1	1	1	1	1	1
Rhyparochromus confusus	0	1	0	0	0	0	0	0
Rhyparochromus phoeniceus	0	0	0	0	1	0	0	0
Rhyparochromus pini	0	0	0	1	1	0	0	0
Rhyparochromus quadratus	1	0	1	1	0	1	1	0
Rhyparochromus vulgaris	0	0	0	0	0	1	0	0
Sciocoris cursitans	0	0	0	1	0	0	0	0
Sciocoris homalonotus	0	0	0	1	0	0	0	0
Sciocoris macrocephalus	0	0	0	0	0	0	1	0
Sciocoris microphthalmus	0	1	0	1	1	0	0	0
Scolopostethus affinis	1	1	0	1	0	0	0	0
Scolopostethus cognatus	0	1	0	0	1	0	0	1
Scolopostethus thomsoni	0	1	0	1	0	0	0	0
Sehirus bicolor	0	0	0	0	0	0	0	1
Sehirus biguttatus	1	0	0	1	1	0	0	0
Sehirus dubius	0	1	0	0	1	1	1	1
Spatocera laticornis	0	0	0	1	0	0	0	0
Staria lunata	0	1	1	1	1	1	1	1
Stenodema calcaratum	1	1	1	1	1	0	0	0
Stenodema laevigatum	1	1	1	1	1	0	1	0
Stenotus binotatus	0	0	0	0	1	0	0	0
Stictopleurus abutilon	1	1	0	1	0	0	0	0
Stictopleurus crassicornis	1	0	1	1	0	0	0	0
Stictopleurus pictus	1	0	1	0	0	0	0	0
Stictopleurus punctatonervosus	1	0	1	1	0	0	0	0
Stygnocoris pygmaeus	0	0	1	0	1	0	0	0
Stygnocoris sabulosus	1	0	1	1	1	0	0	0
Syromastes rhombeus	1	1	0	1	0	0	0	0
Taphropeltus contractus	1	0	1	0	1	0	0	0
Thyreocoris scarabaeoides	1	0	0	0	0	0	0	0
Trigonotylus ruficornis	0	0	0	1	0	0	0	0
Tropidothorax leucopterus	0	1	0	1	1	0	1	1
Tropistethus fasciatus	0	1	1	0	0	0	0	0
Chrysomelidae								
Altica carinthiaca	1	1	1	0	0	1	0	0
Altica oleracea	1	1	1	1	1	1	1	1
Aphthona atrovirens	0	0	0	0	0	1	1	1
Aphthona cyparissiae	0	0	0	0	1	1	0	0
Aphthona herbigrada	0	1	0	1	1	1	1	0
Aphthona ovata	0	0	0	0	0	1	0	1
Aphthona pygmaea	0	0	0	1	0	0	0	0
Aphthona venustula	1	1	1	1	1	1	1	1
Argopus ahrensi	0	0	0	1	0	0	0	0
Asiorestia ferruginea	0	0	0	1	0	0	1	1
Calomicrus circumfusus	0	1	0	0	0	1	0	0
Cassida denticollis	0	1	1	0	0	0	0	0
Cassida margaritacea	1	0	1	0	1	0	0	0
Cassida sanguinolenta	1	1	1	1	1	0	0	0
Cassida subferruginea	0	1	1	0	0	0	0	0
Cassida subreticulata	0	0	0	1	0	0	0	0
Cassida vibex	1	1	1	1	1	1	0	1
Cassida viridis	0	0	1	1	0	0	0	0

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Chaetocnema concinna	0	0	1	0	0	0	0	0
Chaetocnema conducta	1	1	1	1	1	1	1	1
Chaetocnema hortensis	1	1	1	1	1	1	0	1
Chaetocnema laevicollis	1	1	1	1	1	1	0	1
Chaetocnema tibialis	1	0	0	0	0	1	0	0
Chrysolina cerealis	0	1	1	0	1	1	0	0
Chrysolina fastuosa	0	0	0	1	0	0	0	0
Chrysolina haemoptera	1	1	1	1	0	0	1	1
Chrysolina marginata	1	0	1	0	0	0	0	0
Chrysolina oricalcia	0	0	0	1	0	0	0	0
Chrysolina polita	0	0	1	0	0	0	0	0
Chrysolina rossia	0	0	1	0	0	0	0	0
Chrysomela populi	0	0	0	1	0	1	0	0
Clytra appendicina	0	0	0	1	0	0	0	0
Clytra laeviuscula	0	1	1	1	1	1	1	1
Clytra quadripunctata	0	1	0	1	1	1	0	0
Coptocephala scopolina	0	1	0	0	0	0	0	1
Coptocephala unifasciata	0	1	0	1	1	0	0	0
Crepidodera aurata	0	0	0	0	1	0	0	0
Crepidodera aurea	0	1	0	0	0	0	0	0
Crioceris duodecimpunctata	0	1	0	0	0	1	0	0
Cryptocephalus bilineatus	1	1	0	0	1	0	0	0
Cryptocephalus bipunctatus	1	1	0	1	1	1	0	0
Cryptocephalus coryli	0	1	0	0	0	1	0	0
Cryptocephalus elegantulus	1	1	0	1	1	1	0	0
Cryptocephalus flavipes	0	1	1	1	1	1	1	1
Cryptocephalus fulvus	0	0	0	0	1	0	0	0
Cryptocephalus labiatus	0	1	0	1	1	1	1	1
Cryptocephalus loreyi	0	0	0	0	0	0	0	1
Cryptocephalus moraei	0	0	1	1	0	0	1	1
Cryptocephalus nitidus	0	1	1	1	1	1	1	1
Cryptocephalus primarius	0	0	0	0	1	0	0	0
Cryptocephalus pusillus	0	0	1	0	1	0	0	0
Cryptocephalus sericeus	1	1	0	0	1	1	0	0
Cryptocephalus signatifrons	0	0	0	1	1	1	0	1
Cryptocephalus strigosus	1	1	0	1	1	1	1	1
Cryptocephalus transiens	1	1	1	1	1	1	1	0
Cryptocephalus trimaculatus	0	1	0	0	0	0	0	0
Cryptocephalus turcicus	0	1	0	0	0	1	0	0
Cryptocephalus vittula	0	0	1	1	1	0	1	0
Derocrepis sodalis	0	1	1	0	0	0	0	1
Dibolia cryptocephala	0	0	1	1	1	0	0	0
Dibolia foersteri	0	0	0	0	1	0	0	0
Epitrix pubescens	0	1	1	1	0	1	0	0
Eumolpus asclepiadeus	0	0	0	1	1	1	0	0
Exosoma lusitanicum	1	1	1	1	1	1	1	1
Galeruca pomonae	0	0	0	0	0	1	0	0
Galeruca tanaceti	0	1	1	0	1	0	0	0
Gastrophysa viridula	0	0	1	0	0	1	0	0
Hermaeophaga mercurialis	0	0	0	0	0	0	1	1
Labidostomis longimana	0	0	0	0	0	0	0	1
Labidostomis tridentata	0	1	0	0	0	0	0	0
Lachnaia italica	0	1	0	0	0	1	0	0
Leptinotarsa decemlineata	0	1	0	0	0	0	0	0
Lilioceris lilii	0	1	0	0	0	0	0	0
Lilioceris merdigera	0	1	0	0	0	0	0	1
Longitarsus brunneus	1	1	1	1	1	1	0	1
Longitarsus exoletus	0	1	0	1	0	0	0	0
Longitarsus helvolus	0	1	0	1	0	1	1	0
Longitarsus holsaticus	1	0	0	0	0	0	0	0
Longitarsus lewisii	1	0	1	1	0	0	0	1
Longitarsus longiseta	1	0	1	1	0	0	1	1
Longitarsus luridus	1	1	1	1	1	1	1	1
Longitarsus lycopi	0	0	0	1	0	0	0	1
Longitarsus melanocephalus	1	1	1	1	1	0	1	1
Longitarsus minusculus	0	0	0	0	0	0	0	1
Longitarsus niger	0	0	0	1	0	0	1	0
Longitarsus nigrofasciatus	1	1	0	1	0	0	0	0
Longitarsus noricus	0	0	1	0	0	0	1	1

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Longitarsus obliteratus	0	0	0	0	0	1	0	0
Longitarsus pellucidus	0	1	0	0	0	0	0	1
Longitarsus pinguis	0	0	0	0	0	1	0	1
Longitarsus pratensis	1	1	1	1	1	1	1	1
Longitarsus rubiginosus	0	1	1	0	0	0	0	0
Longitarsus salviae	0	0	1	0	0	1	1	1
Longitarsus succineus	1	1	1	1	1	1	1	1
Longitarsus tabidus	0	0	1	0	0	0	0	0
Luperus flavipes	0	1	1	0	1	1	0	0
Luperus leonardii	0	1	0	1	0	0	0	1
Luperus longicornis	1	1	1	1	1	1	1	1
Mantura obtusata	0	1	0	0	0	0	0	0
Oomorphus concolor	0	0	0	0	0	0	0	1
Oulema duftschmidi	1	0	0	0	0	1	0	1
Phyllotreta aerea	0	0	1	0	0	0	0	0
Phyllotreta nemorum	0	0	0	1	0	0	0	0
Phyllotreta ochripes	0	0	1	0	0	0	0	0
Phyllotreta striolata	1	0	0	1	0	0	0	0
Phyllotreta vittula	1	1	1	1	1	1	1	1
Podagrica fuscicornis	1	1	1	0	0	1	0	0
Psylliodes affinis	1	1	1	1	0	0	0	1
Psylliodes brisouti	0	1	0	0	0	0	0	0
Psylliodes cupreus	0	0	0	1	0	0	0	0
Psylliodes dulcamarae	1	1	1	1	0	0	0	1
Psylliodes instabilis	0	1	0	0	0	0	0	0
Psylliodes napi	0	0	1	1	0	0	0	1
Psylliodes toelgi	0	0	0	1	1	1	1	0
Smaragdina affinis	1	1	1	1	1	1	1	0
Smaragdina aurita	1	0	0	0	0	0	0	0
Smaragdina flavicollis	0	0	0	1	0	0	0	0
Smaragdina salicina	1	1	1	1	1	0	1	1
Sphaeroderma rubidum	1	1	1	1	1	1	1	1
Sphaeroderma testaceum	0	0	0	0	0	0	0	1
Timarcha nicaeensis	0	0	1	0	0	0	0	0
Curculionidae								
Anthonomus rubi	1	1	1	1	1	1	0	1
Apion aciculare	1	1	0	0	1	0	0	0
Apion aeneomicans	0	0	0	0	0	1	0	0
Apion aeneuum	1	1	1	0	0	0	0	0
Apion apricans	1	1	1	1	1	1	1	1
Apion armatum	0	1	0	1	1	0	1	0
Apion assimile	1	1	1	1	1	1	1	1
Apion atomarium	0	0	1	1	1	0	0	0
Apion cerdo	0	0	0	0	0	1	0	0
Apion confluens	0	0	1	0	0	0	0	0
Apion cruentatum	0	1	1	1	1	0	1	1
Apion curtirostre	1	1	0	1	1	0	0	0
Apion difficile	1	1	0	0	1	1	0	0
Apion difforme	0	1	0	0	0	0	1	0
Apion ebeninum	0	0	0	0	0	0	1	0
Apion ervi	1	1	1	0	0	1	1	1
Apion filirostre	1	0	0	0	0	0	1	0
Apion flavimanum	0	0	1	0	0	0	0	0
Apion fulvipes	1	1	1	1	1	1	1	0
Apion formaneki	0	1	1	1	1	1	0	0
Apion gyllenhali	0	1	0	0	0	0	0	0
Apion holosericeum	0	0	1	0	0	0	0	0
Apion interjectum	0	1	1	0	0	0	0	0
Apion loti	1	1	1	1	1	1	1	0
Apion minutissimum	0	1	1	0	0	0	0	0
Apion nigritarse	0	0	0	0	0	0	1	0
Apion oblivum	0	0	1	0	0	0	0	0
Apion ononicola	0	1	0	0	0	1	0	0
Apion onopordi	1	1	1	1	1	0	0	1
Apion opeticum	0	0	0	0	0	1	0	0
Apion pavidum	0	1	1	1	0	0	1	1
Apion pisi	1	1	0	1	1	0	1	0
Apion rufirostre	0	0	0	0	0	0	1	0

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Apion seniculus	1	1	1	1	1	1	1	1
Apion simile	0	1	0	1	1	0	0	0
Apion simum	0	1	0	0	1	0	0	0
Apion subulatum	0	0	0	0	1	0	0	0
Apion tenue	0	0	0	1	0	0	1	1
Apion trifolii	1	1	1	1	1	1	1	1
Apion urticarium	0	0	1	1	0	0	0	0
Apion varipes	1	0	1	0	1	1	0	0
Apion viciae	0	1	1	0	0	1	1	0
Apion violaceum	1	1	0	1	1	0	0	0
Apion virens	1	0	1	1	0	0	1	1
Apoderus coryli	1	1	0	1	1	1	0	0
Attelabus nitens	0	1	0	0	0	0	0	0
Balanobius pyrrhoceras	0	1	0	0	1	1	0	0
Baris scolopacea	0	0	0	1	1	0	0	0
Barynotus obscurus	0	1	0	0	0	1	0	0
Ceutorhyncus cochleariae	0	0	1	0	0	0	0	0
Ceutorhyncus contractus	0	0	1	1	1	0	1	1
Ceutorhyncus distinctus	1	1	1	0	1	0	0	0
Ceutorhyncus erysimi	1	1	1	1	0	0	0	0
Ceutorhyncus floralis	1	1	1	1	1	0	0	0
Ceutorhyncus punctiger	1	1	1	0	0	0	0	1
Cionus olivieri	0	0	0	1	1	0	0	0
Cionus thapsus	0	0	1	0	0	0	0	0
Cionus tuberculosus	1	1	0	0	0	0	0	0
Coeliodes dryados	0	1	0	0	0	0	0	0
Coenorhinus aeneovirens	0	0	1	0	0	0	0	0
Coenorhinus germanicus	1	1	1	0	1	1	0	0
Coenorhinus nanus	0	1	0	0	0	1	0	0
Coenorhinus tomentosus	0	1	0	1	1	1	0	0
Curculio glandium	0	1	0	0	1	0	0	0
Curculio nucum	0	1	0	0	1	0	0	0
Donus intermedius	1	1	0	1	0	0	0	0
Donus oxalidis	0	1	0	0	0	0	1	0
Dorytomus taeniatus	1	0	0	0	0	0	0	0
Echinodera hypocrita	0	0	0	0	0	0	0	1
Gymnetron antirrhini	0	1	0	0	1	0	0	0
Gymnetron linariae	1	1	0	0	1	0	0	0
Gymnetron pascuorum	1	1	0	0	1	0	1	0
Gymnetron tetrum	0	0	1	0	0	0	0	0
Homorhythmus hirticornis	1	1	0	0	1	1	1	0
Hypera nigrirostris	0	0	0	0	0	0	1	0
Hypera postica	0	0	0	0	0	0	1	0
Hypera venusta	0	0	0	0	1	0	0	0
Hypera vidua	0	1	0	0	1	0	0	0
Hypera zoilus	0	1	1	0	0	0	0	0
Larinus obtusus	1	1	1	0	1	1	0	0
Larinus sturnus	0	1	1	0	0	0	0	0
Leiosoma concinnum	0	0	0	0	0	0	0	1
Limobius borealis	1	1	0	1	1	1	0	0
Liophloeus tessulatus	0	0	0	0	1	0	0	1
Liparus dirus	0	1	0	0	1	1	1	0
Lixus bardanae	1	0	0	0	0	0	0	0
Magdalis cerasi	0	0	0	0	0	0	0	1
Magdalis exarata	0	0	0	0	0	1	0	0
Mecinus circulatus	1	0	0	0	0	0	0	0
Mecinus pyraster	0	0	1	1	1	0	0	0
Mecinusjanthinus	0	1	0	0	1	0	0	0
Miarus campanulae	0	1	0	0	1	1	0	1
Miarus distinctus	0	1	0	0	0	1	0	0
Miarus graminis	0	1	0	0	1	1	0	1
Miarus micros	0	0	0	0	0	1	0	0
Micrelus ericae	0	0	0	0	1	0	0	0
Mononychus punctumalbum	0	0	0	0	0	1	0	0
Nedyus quadrimaculatus	0	1	1	0	1	0	0	0
Otiorhynchus carmagnolae	0	1	0	0	1	0	0	0
Otiorhynchus ovatus	0	0	0	1	0	0	0	0
Otiorhynchus salicicola	0	0	1	1	0	0	1	1
Otiorhynchus vehemens	0	1	1	0	0	1	1	1

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Pachytychius sparsutus	0	0	0	0	1	1	0	0
Phyllobius argentatus	0	1	1	0	0	0	0	0
Phyllobius chloropus	1	0	0	0	0	1	1	0
Phyllobius etruscus	0	0	1	0	0	0	0	0
Phyllobius pyri	1	1	1	0	1	1	1	1
Phyllobius subdent. roboretanus	0	1	1	0	1	1	0	0
Phyllobius virideaeris padanus	1	1	1	0	1	0	0	0
Polydrusus atomarius	0	0	0	0	0	0	1	0
Polydrusus cervinus	0	1	1	1	1	1	0	0
Polydrusus confluens	1	0	1	0	1	0	0	0
Polydrusus corruscus	0	0	0	0	0	0	1	0
Polydrusus sericeus	0	1	1	1	1	1	1	0
Pseudocleonus grammicus	0	1	1	0	0	0	0	0
Rhinoncus bruchoides	1	1	0	1	0	0	0	0
Rhinoncus pericarpius	1	1	0	1	1	0	0	0
Rhynchaenus signifer	0	1	0	0	0	0	0	0
Rhynchites aethiops	0	0	1	1	1	1	0	0
Sibinia pellucens	0	1	1	1	1	0	0	0
Sibinia viscariae	1	1	1	1	0	0	1	0
Sitona flavescens	0	0	0	0	1	0	0	0

Specie	Stazioni							
	1	2	3	4	5	6	7	8
Sitona hispidulus	1	0	1	0	0	0	1	1
Sitona humeralis	0	0	0	1	1	0	1	0
Sitona puncticollis	1	1	0	0	0	0	0	0
Sitona sulcifrons argutulus	1	1	1	1	1	1	1	1
Sitona suturalis	0	0	0	0	1	0	0	0
Sitona tibialis	0	0	0	0	1	1	0	0
Stasiodis parvulus	1	1	1	1	1	1	0	1
Stereonychus fraxini	0	0	0	0	0	1	1	0
Strophosoma melanogrammum	1	1	0	0	1	0	0	0
Thamiocolus signatus	0	1	0	0	0	0	0	0
Trichosirocalus rufulus	0	0	0	0	0	0	0	1
Trichosirocalus troglodytes	0	0	1	0	1	0	0	1
Tychius cuprifer	1	1	1	0	1	0	0	0
Tychius junceus	0	0	0	0	0	1	0	0
Tychius longicollis	0	1	0	0	0	0	0	0
Tychius picirostris	0	0	1	0	1	0	0	0
Tychius polylineatus	0	0	0	0	1	0	0	0
Tychius schneideri	0	0	0	0	1	1	0	0
Tychius stephensi	1	1	1	1	1	1	0	1
Zacladus geranii	1	1	0	1	1	1	1	1

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Paride Dioli

Gli Eterotteri (Heteroptera) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Nel corso di una ricerca sugli Eterotteri del Monte Barro sono state censite 169 specie, di cui 13 vengono segnalate per la prima volta in Lombardia. Esse sono: *Bothynotus pilosus, Dicyphus annulatus, Phytocoris dimidiatus, Pinalitus atomarius, Heterocordylus tumidicornis, Globiceps horvathi, Driophylocoris flavoquadrimaculatus, Harpocera thoracica, Heterocapillus tigripes, Berytinus minor, Berytinus clavipes, Heterogaster cathariae* e *Megalonotus dilatatus*. Sono state inoltre confrontate mediante una cluster analysis le nove principali stazioni di campionamento delle specie. Dal punto di vista zoogeografico è emerso che la maggior parte delle specie presenta ampia distribuzione in Asia ed Europa, mentre l'elemento mediterraneo è scarsamente rappresentato, anche in relazione all'assenza di piante ospiti stenomediterranee.

Abstract - Bugs (Heteroptera) from Monte Barro (Italy, Lombardy, Lecco).
As a result of a research on the heteropteran fauna (Insecta, Heteroptera) of the Monte Barro (Lombardia, Italy) 169 species have been recorded: thirteen of them (*Bothynotus pilosus, Dicyphus annulatus, Phytocoris dimidiatus, Pinalitus atomarius, Heterocordylus tumidicornis, Globiceps horvathi, Driophylocoris flavoquadrimaculatus, Harpocera thoracica, Heterocapillus tigripes, Berytinus minor, Berytinus clavipes, Heterogaster cathariae* and *Megalonotus dilatatus*) are new for Lombardia. The main sampling sites (sites 1-9) have been compared through a cluster analysis. The biogeographical analysis of the whole heteropteran fauna has been accomplished: most species are large distributed in Asia and Europe. The number of Mediterranean elements is unimportant, owing to the absence of the typical Mediterranean host plants.

Key words: Monte Barro, Heteroptera, geographical distribution.

Negli anni 1989-1992 il Museo di Milano, con l'appoggio del Consorzio del Parco, ha effettuato una serie di raccolte sul Monte Barro, tese soprattutto allo studio degli insetti legati alla vegetazione dei prati e delle boscaglie circostanti. I campionamenti sono stati effettuati inizialmente in numerose stazioni, e, successivamente, concentrati in nove stazioni prative scelte fra quelle maggiormente rappresentative. Fra queste ultime, otto sono ubicate entro i confini del Parco e una immediatamente all'esterno (in località Ca' di Sala).

Tra il copioso materiale raccolto, conservato presso il Museo di Storia Naturale di Milano, vi è anche un lotto di Eterotteri che sono stati preparati a secco oppure conservati in acetone.

L'esame di questo materiale ha portato alla identificazione di 169 specie, tra le quali 13 entità che non erano state ancora segnalate in Lombardia oppure la cui presenza era dubbia anche alla luce di alcune recenti revisioni dei rispettivi gruppi sistematici. Esse sono: *Bothynotus pilosus, Dicyphus annulatus, Phytocoris dimidiatus, Pinalitus atomarius, Heterocordylus tumidicornis, Globiceps horvathi, Driophylocoris flavoquadrimaculatus, Harpocera thoracica, Heterocapillus tigripes, Berytinus minor, Berytinus clavipes, Heterogaster cathariae* e *Megalonotus dilatatus*.

Ma, ciò che più conta, è che la fauna eterotterologica del Monte Barro può considerarsi a tutt'oggi sufficientemente indagata; il cospicuo numero di specie censite, in rapporto all'esigua estensione del Parco, rende merito alla Direzione del medesimo per aver creduto in questa ricerca.

Descrizione sommaria delle Stazioni di raccolta 1-9

Staz. 1 - Sito archeologico in località Piani di Barra, con calpestìo al centro e bosco ai margini; consistente l'elemento prativo con attività di foraggio residua. Specie vegetali interessanti per gli Eterotteri: *Dactylis glomerata, Centaurea nigrescens, Trifolium repens, Achillea spp., Lolium perenne, Vicia spp., Thesium bavaricum.*

Staz. 2 - Sito archeologico in località Piani di Barra, un po' a valle rispetto alla staz. 1; leggera prevalenza di prateria e mantello su prato falciabile, come risposta all'abbandono di una gestione a foraggio già indebolita. Specie vegetali interessanti per gli Eterotteri: *Galium verum, Geranium sanguineum, Festuca rubra, Valeriana collina, Vicia sepium, Teucrium chamaedrys, T.montanum, Vincetoxicum hirsutum.*

Staz. 3 - Conca prativa a monte del Monumento dell'alpino. convivenza di prateria con elementi di prato falciabile ed elementi di disturbo marginale. Specie vegetali interessanti per gli Eterotteri: *Achillea sp., Centaurea spp., Euphorbia cyparissias, Galium album, G:verum, Lathyrus pratensis, Verbascum thapsus, Vicia spp.*

Staz. 4 - Pendio in località S. Michele, in prossimità del sentiero per Pian Sciresa. Prato falciabile in pieno sviluppo con carattere oligo-mesotrofico. Specie vegetali interessanti per gli Eterotteri: *Echium vulgare, Arabis collina, Daucus carota, Peucedanum spp., Vincetoxicum hirsutum.*

Staz. 5 - Pian Sciresa, prato arido con collinetta a brughiera. Inoltre si nota la presenza di prateria a

Brachypodium rupestre. Specie vegetali interessanti per gli Eterotteri: *Calluna vulgaris, Genista germanica, Hieracium sabaudum, Populus tremula, Cytisus emeriflorus, C. scoparius.*

Staz. 6 - Sentiero per la vetta del M.Barro, sopra l'eremo. Si tratta di una prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura, con una notevole presenza dell'elemento pre-nemorale e tendenza a Quercetum pubescentis s.l.. Specie vegetali interessanti per gli Eterotteri: *Centaurea spp., Corylus avellana, Euphorbia spp., Fraxinus ornus, Origanum vulgare, Ostrya carpinifolia, Teucrium montanum, T. chamaedrys, Thesium spp., Vincetoxicum spp.*

Staz. 7 - Località Fornaci Villa, terrazzo inferiore. Prato contornato da bosco con caratteristiche simili a quelle della stazione 8, ma con specie vegetali più eliofile. Specie vegetali interessanti per gli Eterotteri: *Achillea spp., Trifolium spp., Galium mollugo, Heracleum spp., Medicago spp., Peucedanum spp., Pimpinella spp., Trifolium spp., Vicia spp.*

Staz. 8 - Località Fornaci Villa, terrazzo superiore. Prato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili (*Astrantia major, Prunus avium, Geranium nodosum*), in conseguenza dell'esposizione a Nord - Ovest e dell'elemento sciafilo. Specie vegetali interessanti per gli Eterotteri: *Arrenatherum elatior, Astrantia major, Brachypodium rupestre cespitosum, Ononis spinosa.*

Staz. 9 - Superficie prativa al bordo settentrionale del Lago di Annone. Si rilevano aspetti di canneto, prato umido oligotrofico e vegetazione disorganizzata al marginme esterno.

Tabella 1 - Prospetto delle specie raccolte (in neretto le specie esclusivamente o prevalentemente predatrici). Sotto il numero 10 sono raggruppate diverse stazioni nelle quali le raccolte hanno avuto carattere di sporadicità. A = abbondante.

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
SALDIDAE										
Saldula saltatoria				+						
TINGIDAE										
Kalama tricornis	+		+		+			+		
Dictyonota stricnocera		+								
Lasiacantha capucina				+						
Tingis crispata									+	
Tingis reticulata										+
Catoplatus fabricii			+							
Onchochila simplex				+	+					
Dictyla echii		+								
Copium clavicorne	+	+		A	+	+		+		+
Agramma laetum									+	
MIRIDAE										
Bothynotus pilosus										+
Bryocoris pteridis						+				
Deraeocoris annulipes				+			+	+		
Deraeocoris ruber		+			+					+
Deraeocoris serenus	+	+		+						
Dicyphus flavoviridis	+		+							+
Dicyphus globulifer	+		+							+
Dicyphus annulatus					+					
Stenodema sericans										+
Stenodema calcaratum	+	+	+	+	+				+	
Stenodema laevigatum	+	+	A	+	+		+		+	+
Trigonotylus ruficornis				+						
Notostira erratica			+	A				+		
Megaloceroea recticornis		+		+	+					
Phytocoris dimidiatus						+				
Adelphocoris lineolatus		+	+	A	+		+	+		+
Adelphocoris seticornis	+	+	+					A	+	+
Adelphocoris vandalicus					+					+
Calocoris striatellus			+		+	+				A
Stenotus binotatus					+					
Pantilius tunicatus		+		+						
Exolygus pratensis	+	+	+	+				+	+	+
Pinalitus atomarius				+						
Orthops kalmi		+	A		+	+				+
Liocoris tripustulatus			+	+	+				+	
Polymerus holosericeus									+	
Polymerus unifasciatus		+	+	A	A	+		+	A	+
Capsus ater	+		+		+				+	
Halticus apterus	+		+	+	+			A	A	
Heterocordylus genistae		A		+	A	+				
Heterocordylus tumidicornis								+		
Globiceps horvathi			A		+	A				
Globiceps sphaegiformis		+		+						+
Dryophylocoris flavoquadrimaculatus	+	+	A			+				+
Cyllecoris histrionicus	+									
Pilophorus perplexus				+						+
Pilophorus clavatus	+		+		+					
Harpocera thoracica	A		+			+				+
Phylus coryli				+						
Chlamidatus pulicarius	A	+	A	+			+		+	
Plagiognathus arbustorum										+
Criocoris crassicornis		+		+						
Heterocapillus tigripes										+
Psallus variabilis	+			+	+					+
Charagochilus gyllenhali	+	+	A	A		+	+	+	+	+
Charagochilus weberi			+			+				
NABIDAE										
Prostemma aeneicolle		+								
Himacerus apterus								+		+
Aptus mirmicoides	+	A	+	A	+	+	+	+	+	+
Nabis rugosus	A	A	+	+	A	+	+	+	+	+
Nabis punctatus	+		+	+	+			+	+	
ANTHOCORIDAE										
Anthocoris confusus			+							
Anthocoris nemoralis	+									
Anthocoris nemorum		+								+
Orius majusculus				+					+	
Orius niger	A	+	+				+	+		

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
PHYMATIDAE										
Phymata crassipes		+		+						+
REDUVIIDAE										
Rhynocoris iracundus		+								
Rhynocoris annulatus						+		+		
ARADIDAE										
Aradus depressus										+
BERYTIDAE										
Berytinus minor				+				+		
Berytinus clavipes				+	+					
LYGAEIDAE										
Tropidothorax leucopterus		A		+	A		+	+		+
Lygaeus equestris	+	A	A		+	+				+
Lygaeus saxatilis				+						
Nysius senecionis	+			+		+				
Nysius ericae				+						+
Nisius thymi				+						
Kleidocerys resedae	+	A		+	A					+
Cymus aurescens						+				
Ischnodemus quadratus		+							A	+
Geocoris megacephalus	+									
Oxycarenus pallens	+	A			+	+				
Oxycarenus lavaterae										+
Macroplax preyssleri	A	A		+	+	+		+		+
Macroplax fasciatus	+				+		+			+
Heterogaster cathariae	+									
Platyplax salviae	+		+	+			+			+
Plinthisus brevipennis				+						
Tropistethus fasciatus		+	+							
Drymus sylvaticus	+	+		+				+		
Drymus ryeii		+								
Scolopostethus affinis	+	A		+						
Scolopostethus decoratus									+	
Scolopostethus cognatus		+			+			+		
Scolopostethus thomsoni		+		+						
Taphropeltus contractus	+		+		+					
Acompus rufipes		A								
Stygnocoris sabulosus	+		+	+	+					
Stygnocoris pygmaeus			A		+					
Pachybrachius fracticollis									A	
Beosus maritimus		+	+	A						+
Aellopus atratus		+								
Rhyparochromus quadratus	A		+	A		+	+			
Rhyparochromus alboacuminatus										+
Rhyparochromus confusus		+								
Rhyparochromus vulgaris						+				
Rhyparochromus phoeniceus					+					+
Rhyparochromus pini				+	+					
Peritrechus geniculatus	A		A	A	+		+		+	
Peritrechus gracilicornis	+		+	+	+		+		+	
Paromius leptopoides	+				+					
Megalonotus praetextatus	+									
Megalonotus antennatus								+		
Megalonotus dilatatus					+					
Emblethis verbasci	+	+					+			
PYRRHOCORIDAE										
Pyrrhocoris apterus	A		+							
COREIDAE										

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Enoplops scapha	+	+			+	+			+	
Coreus marginatus	+	A					+	+		
Syromastes rhombeus	+	+		+					+	
Gonocerus acuteangulatus		+				+				
Spatocera laticornis				+						
Coriomeris scabricornis			+	+						
Coriomeris denticulatus	+		+	+						
ALYDIDAE										
Alydus calcaratus	A		+	+	+			+	+	+
RHOPALIDAE										
Corizus hyoscyami		+	+	+			+	+		
Rhopalus maculatus									+	
Rhopalus parumpunctatus	+	+	+	+						
Rhopalus conspersus		+	+	A	+	+	+			+
Rhopalus subrufus	+	+	+	+	+	+	+	+		+
Stictopleurus pictus	+		+							
Stictopleurus abutilon	+	+		+						
Stictopleurus crassicornis	A		A	+					+	+
Stictopleurus punctatonervosus	A		+	+					+	+
CYDNIDAE										
Sehirus bicolor								+		+
Sehirus biguttatus	+			+	+					
Sehirus dubius		+			+	A	A	+		+
Legnotus limbosus		+	+	+					+	+
Legnotus picipes				+						
Thyreocoris scarabeoides	+									
SCUTELLERIDAE										
Odontotarsus purpureolineatus		+				+				+
Eurygaster maurus	+	A	+	+	+					+
Eurygaster testudinarius	+				A		+	+	A	
PENTATOMIDAE										
Graphosoma lineatum		A		+					+	+
Podops inuncta	+	+			+				+	
Sciocoris cursitans				+						
Sciocoris macrocephalus							+			
Sciocoris homalonotus				+						
Sciocoris microphthalmus		+		A	+					
Aelia acuminata	+	+		+					+	+
Eysarcoris aeneus		+			+				A	
Staria lunata		+	+	+	+	+	+	+		+
Dryocoris vernalis		+		+	+		+		+	
Dryocoris sphacelatus		+		+						+
Carpocoris pudicus		A	+		+	+	+	+		+
Dolycoris baccarum	+	A	+	+	+		+	+	+	+
Eurydema ornatum				+						
Eurydema ventrale				+						
Eurydema oleraceum	+	+	+	A	+		+	+	+	+
Piezodorus lituratus	+	+			+	+	+			
Palomena prasina		+			+					+
Nezara viridula							+		+	+
Raphigaster nebulosa									+	
Pentatoma rufipes	+	+								
Picromerus bidens		+		+						
Zicrona coerulea				+						
ACANTHOSOMIDAE										
Acanthosoma haemorrhoidale		+								
PLATASPIDAE										
Coptosoma scutellatum		A	+	+		+			+	+

L'analisi del popolamento emitterologico viene fatta attraverso l'individuazione dei rapporti gerarchici di somiglianza fra le prime nove stazioni di raccolta degli eterotteri. Tali rapporti sono evidenziati nel dendrogramma di Fig. 5 che è stato ottenuto utilizzando l'indice di Sorensen e la cluster analysis secondo il metodo WPGMA. La matrice per l'analisi, che qui non si riporta, è facilmente ricavabile dalla tabella soprastante.

Come si può osservare, le Staz. 1, 2, 3, 4 fanno gruppo assieme e rappresentano un «cluster» ben identificato dalle situazioni a prato degradato che richiamano eterotteri antropofili.

La Staz. 5 si stacca nettamente per la presenza della tipica fauna degli eterotteri di brughiera.

La Staz. 6 (sotto la vetta del Barro) è quella più povera di specie (forse a causa di una certa ventosità) ed è perciò molto distante dalla precedente.

Le Staz. 7 e 8 hanno invece una somiglianza che viene molto ben enfatizzata dal dendrogramma. Guardando la situazione in loco, scopriamo infatti che esse sono entrambe caratterizzate dalla vicinanza della faggeta, un fattore che risulta determinante anche in altri studi entomologici di questa serie sul Parco del Barro.

La Staz. 9, infine, pur avendo delle affinità con il primo gruppo (1, 2, 3, 4) se ne discosta in forza della presenza di alcuni elementi igrofili legati alle specie vegetali tipiche di ambienti umidi.

Discussione delle specie

Saldidae

1. ***Saldula saltatoria*** (Linné, 1758)
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni settentrionali, meno frequente al Sud dove è presente solo in montagna.
Biologia: predatore di microinvertebrati. Specie opportunista che può adattarsi bene sia in riva a piccoli ruscelli che sulle spiagge marine.

Tingidae

2. ***Kalama tricornis*** (Schrank, 1801)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni.
Biologia: solitamente su *Artemisia campestris*.

3. ***Dictyonota strichnocera*** Fieber, 1844
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, qua e là in quelle centro meridionali e in Sicilia, assente in Sardegna.
Biologia: su *Cytisus* spp., *Ulex europaeus*, *Genista* spp..

4. ***Lasiacantha capucina*** (Germar, 1836)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: regioni settentrionali e centrali, sino all'Abruzzo.
Biologia: su *Thymus* spp., *Salvia* spp., *Teucrium* spp..

5. ***Tingis crispata*** (Herrich - Schaffer, 1838)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: regioni settentrionali.
Biologia: *Arthemisia* spp..

6. ***Tingis reticulata*** (Herrich - Schaffer, 1835)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni settentrionali e centrali.
Biologia: *Ajuga* spp..
Note di raccolta: l'insetto è stato raccolto in un prato vicino alla staz. 4 (loc. S. Michele).

7. ***Catoplatus fabricii*** (Stal, 1868)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni settentrionali. In quelle centro-meridionali, solo in Abruzzo, Puglie e Basilicata.
Biologia: su *Leucanthemum vulgare, Chrysanthemum* spp.

8. ***Onchochila simplex*** (Herrich - Schaffer, 1830)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: nelle regioni settentrionali.
Biologia: su *Euphorbia* spp.

9. ***Dictyla echii*** (Schrank, 1782)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Biologia: *Echium* spp.

10. ***Copium clavicorne*** (Linné, 1758)
Corotipo: S-Europeo (SEU).
Presenza in Italia: regioni settentrionali e, scendendo al Sud, sull'Appennino.
Biologia: *Teucrium chamaedrys*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

11. ***Agramma laetum*** (Fallén, 1807)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni settentrionali, meno comune al centro-sud.
Biologia: in ambienti umidi su *Juncus* spp., *Carex* spp.

Miridae

12. ***Bothynotus pilosus*** (Boheman, 1852), Fig. 1
Corotipo: Europeo (EUR).
Presenza in Italia: segnalato di alcune regioni settentrionali (Piemonte, Liguria, Trentino, Friuli Venezia Giulia) e Sicilia. Prima citazione per la Lombardia.
Biologia: nelle radure e brughiere, più raramente nei boschi di *Pinus*, generalmente legato a *Calluna vulgaris*.
Note di raccolta: l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.
Note geonemiche: se si eccettua il dato più recente, relativo al Friuli, citato da Servadei (1967), le segnalazioni italiane per questa specie risalgono tutte al secolo scorso. Considerando che il *Bothynotus pilosus* (Boheman, 1852) presenta la femmina brachittera, ne consegue una naturale propensione all'isolamento e alla localizzazione in aree con calluneti relitti. In questo contesto, assume notevole importanza il reperto proveniente dal Monte Barro, che potrebbe configurarsi come stazione relitta per questa specie.

13. ***Briocoris pteridis*** Fallén, 1807
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni alpine.
Biologia: su felci, particolarmente *Pteridium aquilinum*.
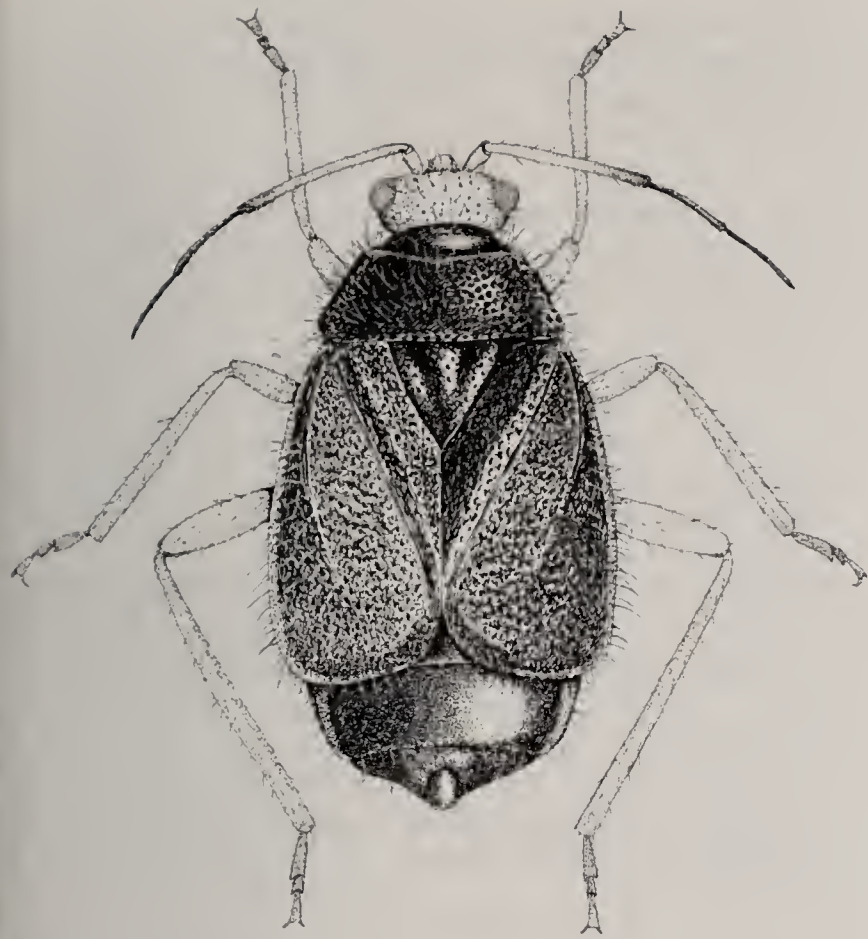
Fig. 1 - *Bothynotus pilosus* (disegno di C. Pesarini).

14. ***Deraeocoris annulipes*** (Herrich - Schaffer, 1845)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni alpine.
Biologia: predatore, su *Larix* o *Picea* infestati da afidi.

15. ***Deraeocoris ruber*** (Linné, 1758)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: su svariate latifoglie ma anche aghifoglie, infestate da afidi o psillidi.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che che dall'eremo va alla Sella della Pila.

16. ***Deraeocoris serenus*** Douglas & Scott, 1868
Corotipo: Mediterraneo (MED).
Presenza in Italia: tutte le regioni.
Biologia: predatore di microinsetti su svariate piante erbacee.

17. ***Dicyphus flavoviridis*** Tamanini, 1949
Corotipo: Endemico italiano (END).
Presenza in Italia: tutte le regioni.
Biologia: *Rubus* spp., *Geranium* spp., *Galeopsis* spp..
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nel sottobosco della Val Faè.

18. ***Dicyphus globulifer*** (Fallén, 1829)
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni.
Biologia: su *Chrysanthemum* spp., *Lycnis* spp., *Melandryum* spp., *Ononis* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato presso Camporeso.

19. ***Dicyphus annulatus*** (Wolff 1804)
Corotipo: Europeo (EUR).
Presenza in Italia: nelle regioni settentrionali è sporadica e si hanno dati certi solo di Piemonte e Liguria. Più comune al Sud, ma la sua distribuzione necessita di conferma dopo la separazione da *D. ononidis* E.Wagner, 1951. Prima citazione per la Lombardia.
Biologia: su *Ononis spinosa*.
Note sistematiche: *D. annulatus* si distingue da *D. ononidis* E.Wagn, 1951, per le dimensioni del secondo articolo antennale decisamente più corto. Esso è infatti di poco più lungo del terzo e la metà della larghezza del pronoto. *D. ononidis* ha invece il secondo articolo antennale che è 0,7-0,8 volte la larghezza del pronoto.

20. ***Stenodema sericans*** (Fieber, 1861)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni settentrionali e, alle quote più elevate, in quelle appenniniche e in Sicilia.
Biologia: poacee.
Note di raccolta: l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

21. ***Stenodema calcaratum*** (Fallén, 1807)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Biologia: su diverse Poacee.

22. ***Stenodema laevigatum*** (Linné, 1758)
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni.
Biologia: poacee (spesso svernante su conifere).
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nel sottobosco della Val Faè.

23. ***Trigonotylus ruficornis*** (Geoffroy, 1785)
Corotipo: Olartco (OLA).
Presenza in Italia: tutte le regioni.
Biologia: su poacee, preferibilmente in ambienti umidi.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato vicino alla staz. 4 (loc. S. Michele).

24. ***Notostira erratica*** (Linné, 1758)
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni.
Biologia: poacee.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nel sottobosco della Val Faè.

25. ***Megaloceroea recticornis*** (Geoffroy, 1785)
Corotipo: Europeo - Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: Poacee, preferibilmente *Triticum* spp..

26. ***Phytocoris dimidiatus*** (Kirschbaum, 1856)
Corotipo: Europeo - Mediterraneo (EUM).
Presenza in Italia: Piemonte, Liguria, Trentino, Lazio e Sicilia. Prima segnalazione per la Lombardia.
Biologia: predatore di microinsetti su latifoglie (*Pirus, Malus, Quercus*), ma anche su *Pinus* spp..

27. ***Adelphocoris lineolatus*** (Goeze, 1778)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Biologia: *Artemisia* spp., *Verbascum* spp., *Achillea* spp., *Medicago* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato presso Camporeso.

28. ***Adelphocoris seticornis*** (Fabricius, 1775)
Corotipoo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni. Dubbia la presenza sulle isole maggiori (Faraci & Rizzotti, 1995).
Biologia: su papilionacee, come *Medicago* spp., *Trifolium* spp., *Vicia* spp.. Adulti soprattutto in luglio e agosto.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto sulla vegetazione ai margini della strada asfaltata che sale verso il Monumento all'Alpino.

29. ***Adelphocoris vandalicus*** (Rossi, 1790)
Corotipo: Mediterraneo (MED).
Presenza in Italia: tutte le regioni, ma raro in quelle alpine
Biologia: *Verbascum* spp., *Achillea* spp., *Arthemisia* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella d. Pila.

30. ***Calocoris striatellus*** (Fabricius, 1794) (= *C. quadripunctatus*, Vill., 1789)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: su *Quercus* sp., dove si comporta talora da zoofago, talora da fitofago.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

31. ***Stenotus binotatus*** (Fabricius, 1794)
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni, tranne la Sardegna.
Biologia: *Melilotus* spp., *Medicago* spp..

32. ***Pantilius tunicatus*** (Fabricius, 1781)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, raro al Sud.
Biologia: *Betula* spp., *Corylus* spp.

33. ***Exolygus pratensis*** (Linné, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: su svariate piante erbacee tra cui *Urtica* spp., *Artemisia* spp., *Stachys* spp. e *Mentha* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato vicino alla staz. 4 (loc. S. Michele).

34. ***Pinalitus atomarius*** (Meyer - Dur, 1843)
Corotipo: S-Europeo (SEU).
Presenza in Italia: Trentino, Piemonte, Emilia, Lazio e Calabria. Prima segnalazione per la Lombardia.
Biologia: sulle conifere.

35. ***Orthops kalmi*** (Linné, 1758)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Biologia: su Apiacee come *Peucedanum* spp., *Pimpinella* spp., *Daucus* spp., *Pastinaca* spp. ecc.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nei prati sotto Sella d. Pila, a circa 700 m di quota.

36. ***Liocoris tripustulatus*** (Fabricius, 1781)
Corotipo: Paleartica (PAL).
Presenza in Italia: tutte le regioni.
Biologia: su *Parietaria* spp., *Solanum* spp., *Urtica* spp., *Verbascum* spp., *Salvia* spp.

37. ***Polymerus holosericeus*** (Hahn, 1831)
Corotipo: Turanico-Mediterraneo (TUM).
Presenza in Italia:regioni montane delle Alpi e dell'Appennino, sino alla Campania.
Biologia: su *Urtica* spp. e *Galium* spp.

38. ***Polymerus unifasciatus*** (Fabricius, 1794)
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni.
Biologia: *Galium* sp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

39. ***Capsus ater*** (Linné, 1758)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: su *Phleum* spp.

40. ***Halticus apterus*** (Linné, 1758)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: *Ononis* spp., *Galium* spp.

41. ***Heterocordylus genistae*** (Scopoli, 1763)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, centro-meridionali e Sardegna.
Biologia: *Genista* spp.; regime dietetico solo parzialmente fitofago.

42. ***Heterocordylus tumidicornis*** (Herrich - Schaffer, 1836)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: diverse regioni settentrionali, centrali e meridionali. Prima segnalazione per la Lombardia.
Biologia: soprattutto su *Prunus* spp.e *Mespilus germanica*, ma anche su *Alnus* spp., *Euonimus europaeus* e *Sarothamnus scoparius*; regime dietetico solo parzialmente fitofago.

43. ***Globiceps horvathi*** Reuter, 1912
Corotipo: Est-Mediterraneo (EME).
Presenza in Italia: le citazioni sicure sono di Piemonte, Trentino, Alto Adige, Marche, Abruzzo, Campania, Calabria e Sicilia. Prima segnalazione per la Lombardia.
Biologia: su *Ononis* spp., *Spartium* spp., *Galium* spp., *Corylus* spp., *Crataegus* spp.

44. ***Globiceps shaegiformis*** (Rossi, 1790)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: soprattutto su *Quercus* spp., ma talora anche su *Acer campestre* e *Corylus avellana*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

45. ***Driophylocoris flavoquadrimaculatus*** (De Geer, 1773)
Corotipo: Europeo-Mediterraneo (EUM).

Presenza in Italia: si hanno segnalazioni sicure di Piemonte, Trentino, Alto Adige, Veneto, Emilia, Umbria, Lazio, Puglia e Sicilia. Prima segnalazione per la Lombardia.
Biologia: fitofago e zoofago su *Quercus* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila e in un prato presso Camporeso.

46. ***Cyllecoris histrionicus*** (Linné, 1767)
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni.
Biologia: su *Quercus* sp.; regime dietetico zoofago e fitofago.

47. ***Pilophorus perplexus*** Dgl.& Scott, 1785 (= *P.pusillus* Reuter, 1878)
Corotipo: Europeo - Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: predatore di afidi su *Prunus* spp., *Juniperus* spp. e *Alnus glutinosa*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

48. ***Pilophorus clavatus*** (Linné, 1767)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni centro settentrionali, più raro al Sud.
Biologia: predatore di afidi su *Populus* spp.

49. ***Harpocera thoracica*** (Fallén, 1807)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: Piemonte, Veneto, Friuli-Venezia Giulia, Liguria, Umbria e Sicilia. Prima segnalazione per la Lombardia.
Biologia: su *Quercus*; forme giovanili essenzialmente fitofaghe, adulti anche predatori di microinsetti; nelle Prealpi legato al «*Querco-Betuletum insubricum*» (Dioli, 1993).
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato presso Camporeso.

50. ***Phylus coryli*** (Linné, 1758)
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni settentrionali, centro-meridionali e Sicilia.
Biologia: su *Corylus avellana*, anche predatore di microinsetti.

51. ***Chlamidatus pulicarius*** (Fallén, 1807)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni settentrionali e lungo l'Appennino sino al Molise.
Biologia: su *Artemisia* spp., *Achillea* spp.

52. ***Plagiognathus arbustorum*** (Fabricius, 1794)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Biologia: comune soprattutto su *Urtica* spp.
Note di raccolta: l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

53. ***Criocoris crassicornis*** (Hahn, 1834)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: regioni settentrionali, Emilia, Liguria, Umbria, Abruzzo e Sicilia.
Biologia: su *Galium* spp.

54. ***Heterocapillus tigripes*** (Mulsant, 1852)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, Emilia, Toscana, Abruzzo e Molise, Campania, Basilicata e Calabria. Prima segnalazione per la Lombardia.
Biologia: su *Dorycnium* spp.
Note di raccolta: l'insetto è stato raccolto ai margini di un sentiero che dall'eremo va alla Sella della Pila.

55. ***Psallus variabilis*** (Fallén, 1807)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Trentino, Alto Adige, Veneto, Lombardia, Piemonte, Emilia, Calabria, Puglia.
Biologia: su *Prunus spinosa*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila.

56. ***Charagochilus gyllenhali*** (Fallén, 1807)
Corotipo: Paleartico (PAL).
Presenza in Italia: Piemonte, Lombardia, Alto Adige, Trentino, Veneto, Emilia, Marche, Umbria, Abruzzo, Calabria, Sicilia.
Biologia: su *Galium* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato della Val Faè attiguo alla staz. 7, in un prato in località S. Michele vicino alla staz. 4 e in un prato vicino a Camporeso.

57. ***Charagochilus weberi*** E.Wagner, 1953
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Alto Adige, Veneto, Marche, Umbria, Abruzzo, Campania, Puglie, Sicilia e Montecristo.
Biologia: su *Verbascum* spp.

Nabidae

58. ***Prostemma aeneicolle*** Stein, 1857
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino, Alto Adige, Lombardia, Veneto, Liguria, Emilia, Toscana, Abruzzo e Molise, Calabria.
Biologia: prevalentemente predatore di eterotteri ligeidi e pentatomidi.

59. ***Himacerus apterus*** (Fabricius, 1798)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e centrali, raro al Sud.
Biologia: si nutre prevalentemente di afidi e larve di lepidotteri sulle latifoglie.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nel sottobosco della Val Faè.

60. ***Aptus mirmicoides*** (O.Costa, 1834)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: predatore di microinsetti su erbe basse e arbusti.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila, in un prato della val Faè vicino alla staz. 7, lungo un sentiero che dall'eremo conduce alla Sella della Pila e in un prato presso Camporeso.

61. ***Nabis rugosus*** (Linné, 1758)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: regioni alpine, più raro in quelle appenniniche, assente nelle isole.

Biologia: predatore di afidi e microinsetti, generalmente su *Artemisia* spp. ed *Erica* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato vicino a Camporeso.

62. ***Nabis punctatus*** (Costa, 1847)
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutte le regioni.
Biologia: predatore di microinsetti sulle erbe basse e sugli arbusti, spesso associato a *Stenodema* spp.

Anthocoridae
63. ***Anthocoris confusus*** Reuter, 1884
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni alpine, Emilia, Umbria, Lazio, Abruzzo e Molise, Basilicata, Sicilia.
Biologia: predatore di microinsetti su *Betula* spp. e *Fagus* spp.

64. ***Anthocoris nemoralis*** (Fabricius, 1794)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: predatore di microinsetti, specialmente psille e afidi, su *Crataegus* spp., *Sorbus* spp., *Euphorbia* spp., *Fraxinus* spp., *Populus* spp., *Rhamnus* spp., *Prunus* spp.

65. ***Anthocoris nemorum*** (Linné, 1761)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: predatore di psillidi e afidi su *Picea* spp., *Alnus* spp., *Salix* spp., ma anche su piante erbacee come *Urtica* spp. e *Daucus carota*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto lungo un sentiero che dall'eremo conduce alla Sella della Pila.

66. ***Orius majusculus*** (Reuter, 1879)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Trentino, Alto Adige, Veneto, Emilia, Marche, Toscana, Abruzzo, Calabria, Sardegna.
Biologia: predatore di microinsetti (afidi, larve di microlepidotteri) e acari, soprattutto in ambienti umidi su *Polygonum* spp., *Phragmites* spp. e *Carex* spp.

67. ***Orius niger*** (Wolff, 1811)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: predatore di microinsetti (afidi, tisanotteri) e acari su *Artemisia* spp., *Achillea* spp., *Verbascum* spp.

Phymatidae
68. ***Phymata crassipes*** (Fabricius, 1775)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: predatore, generalmente sui fiori o tra le erbe secche in ambienti soleggiati.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto lungo un sentiero che dall'eremo conduce alla Sella d. Pila.

Reduviidae
69. ***Rhynocoris iracundus*** (Poda, 1761)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni, anche in montagna. Meritano conferma le segnalazioni per la Sardegna.
Biologia: predatore di invertebrati.

70. ***Rhynocoris annulatus*** (Linné, 1758)
Corotipo: Sibirica-Europeo (SIE).
Presenza in Italia: tutte le regioni dalle Alpi alla Calabria. Dubbia la presenza in Sicilia, assente in Sardegna.
Biologia: predatore di invertebrati, è la specie di *Rhynocoris* che si spinge più in alto in montagna: nella zona alpina è stato trovato a 2500 metri di altezza (Passo Forcola di Livigno), in ambienti asciutti e steppici.

Aradidae
71. ***Aradus depressus*** (Fabricius, 1794)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni peninsulari e la Sicilia.
Biologia: si nutre del micelio e dei corpi fruttiferi di poliporacee attaccate a *Betula, Quercus e Fagus.*

Berytidae
72. ***Berytinus minor*** (Herrich - Schaffer, 1835)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Trentino, Alto Adige, Emilia, Abruzzo, Lazio, Sardegna. Prima segnalazione per la Lombardia.
Biologia: specie legata principalmente a *Trifolium* spp. e *Medicago* spp.

73. ***Berytinus clavipes*** (Fabricius, 1775)
Corotipo: Sibirico - Europeo (SIE).
Presenza in Italia: Piemonte, Trentino, Veneto, Emilia, Toscana. Prima segnalazione certa per la Lombardia, dopo la revisione di Pericart (1984).
Biologia: *Ononis* spp., *Vicia* spp.

Lygaeidae
74. ***Tropidothorax leucopterus*** (Goeze, 1778)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: su *Vincetoxicum* spp. e *Cynanchum* spp..
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto lungo un sentiero che dall'eremo conduce alla Sella d. Pila e in un prato vicino a Camporeso.

75. ***Lygaeus equestris*** (Linné, 1758)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni, tranne la Sicilia.
Biologia: in prevalenza su *Artemisia*, *Achillea*, *Medicago*, *Trifolium*, *Scrophularia* e *Datura*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila (m 700), nei boschi della Val Faè e lungo un sentiero che dall'eremo conduce alla Sella della Pila.
Note geonemiche: la descrizione recente della specie affine, *Lygaeus simulans* (Deckert, 1985), ha portato ad una ridefinizione della distribuzione generale di *L. equestris*, sotto il cui nome erano precendentemente confuse le due entità.
L. simulans, in Italia, si comporta come elemento prevalentemente montano nelle Alpi e sull'Appennino mentre *L. equestris* è specie più ubiquista.
Note sistematiche: il carattere che consente l'im-

mediata separazione delle due specie risiede nello scutello: glabro o con micro-peli in *L. equestris*, irsuto con peli lunghi ed eretti in *L. simulans*. Interessante anche la possibilità di facile separazione delle due specie negli stadi larvali: su *Cynanchum* sono state osservate neanidi del 5° stadio di *L. simulans* (color avorio con striature rosse) e di *L. equestris* (completamente rosse). (Melber & Coll., 1991).

76. ***Lygaeus saxatilis*** (Scopoli, 1763)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: specialmente su *Colchicum autumnale*.

77. ***Nysius senecionis*** (Schilling, 1828)
Corotipo: Turanico-mediterraneo-Europeo (TEM).
Presenza in Italia: tutte le regioni, meno comune al Sud.
Biologia: su *Artemisia absinthium*.

78. ***Nysius ericae*** (Schilling, 1829)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e, più sporadico, in quelle meridionali.
Biologia: *Artemisia* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato vicino a Camporeso.

79. ***Nysius thymi*** (Wolff, 1804)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni, al Sud, solo sui monti.
Biologia: *Artemisia* spp.

80. ***Kleidocerys resedae*** (Panzer, 1789)
Corotipo: Sibirico-Europeo (SIE) e Neartico.
Presenza in Italia: regioni settentrionali, Emilia e Toscana.
Biologia: *Betula* spp., *Calluna vulgaris*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato della val Faè vicino alla staz. 7.

81. ***Cymus aurescens*** Distant, 1883 (= *obliquus* Horvath, 1888)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Piemonte, Lombardia, Trentino e Liguria.
Biologia: su *Scirpus* spp.

82. ***Ischnodemus quadratus*** (Fieber, 1836)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni italiane
Biologia: poacee, in zone umide o paludose.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato vicino alla staz. 4.

83. ***Geocoris megacephalus*** (Rossi, 1790)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni. Le vecchie citazioni di *G. siculus* (Fieber) 1844, si riferiscono in realtà a questa specie (Tamanini, 1981).
Biologia: detriti di *Artemisia* spp.

84. ***Oxycarenus pallens*** (Herrich - Schaffer, 1850)
Corotipo: Centroasiatico-Mediterraneo (CAM).
Presenza in Italia: tutte le regioni, raro nelle Alpi.
Biologia: su *Centaurea* spp.

85. ***Oxycarenus lavaterae*** (Fabricius, 1787)
Corotipo: Mediterraneo (MED).
Presenza in Italia: tutte le regioni, spesso in folte colonie gregarie sulle piante ospiti, dove riesce talvolta dannoso.
Biologia: soprattutto sul tiglio (*Tilia cordata*), fitofago e, nei mesi invernali o di rifugio, corticicolo.
Note di raccolta: ne sono stati raccolti numerosi esemplari in una radura sotto l'eremo.

86. ***Macroplax preyssleri*** (Fieber, 1838)
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni peninsulari e Sicilia, raro sulle Alpi.
Biologia: *Thymus serpyllum*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto lungo un sentiero che dall'eremo conduce alla Sella della Pila.

87. ***Macroplax fasciatus*** (Herrich - Schaffer, 1835)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni, al Sud sino a 2000 m.
Biologia: *Ononis* spp., *Cistus* spp., *Spartium junceum*.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto nei prati sotto la Sella d. Pila (m 700) e lungo un sentiero che dall'eremo conduce alla Sella della Pila.

88. ***Heterogaster cathariae*** (Geoffroy, 1785), Fig. 2
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: specie rara, sicuramente pre-

Fig. 2 - *Heterogaster cathariae* (disegno di C. Pesarini).

sente in Piemonte, Trentino e in Alto Adige. A queste citazioni posso aggiungere l'Emilia (Casola!) per un esemplare raccolto su *Nepeta catharia*. Nuova segnalazione per la Lombardia.
Biologia: specie infeudata su *Nepeta catharia*, più raramente su *Mentha* spp., *Melissa* spp., *Lycopus* spp.

89. ***Platyplax salviae*** (Schilling, 1829)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali e centrali, sino alla Toscana e l'Umbria.
Biologia: su *Salvia* spp.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto lungo un sentiero che dall'eremo conduce alla Sella della Pila.

90. ***Plinthisus brevipennis*** (Latreille, 1807)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: detriti di Ericacee.

91. ***Tropistethus fasciatus*** Ferrari, 1874
Corotipo: Mediterraneo (MED).
Presenza in Italia: Trentino, Veneto, Lombardia, Emilia, Umbria, Lazio e Sicilia.
Biologia: ambienti asciutti con detriti vegetali.

92. ***Drymus sylvaticus*** (Fabricius, 1775)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni, ma raro al Sud. Non segnalato di Sardegna.
Biologia: detriti di latifoglie.

93. ***Drymus ryeii*** (Douglas & Scott, 1865).
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Valle d'Aosta, Lombardia, Veneto, Trentino e Venezia Giulia. Da confermare le segnalazioni per la Sicilia.
Biologia: detriti di latifoglie o sotto pietre.

94. ***Scolopostethus affinis*** (Schilling, 1829)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni settentrionali e centrali sino all'Abruzzo.
Biologia: detriti di *Urtica* e latifoglie.

95. ***Scolopostethus decoratus*** (Hahn, 1833)
Corotipo: Europeo-Mediteraneo (EUM).
Presenza in Italia: tutte le regioni.
Biologia: detriti di Ericacee.

96. ***Scolopostethus cognatus*** (Fieber, 1861)
Corotipo: Mediteraneo (MED).
Presenza in Italia: regioni centro-meridionali e Sardegna, raro però nella zona alpina dove è infeudato alle zone xerotermiche o, comunque, molto soleggiate.
Biologia: *Calluna vulgaris*, *Erica arborea*.

97. ***Scolopostethus thomsoni*** Reuter, 1874
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni e Sardegna.
Biologia: detriti di *Urtica* spp.

98. ***Taphropeltus contractus*** (Herrich - Schaffer, 1839)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni, anche se piuttosto raro ovunque.
Biologia: detriti di latifoglie.

99. ***Acompus rufipes*** (Wolff, 1804)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni, tranne le isole.
Biologia: *Valeriana officinalis*.

100. ***Stygnocoris sabulosus*** (Schilling, 1829)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni settentrionali, appenniniche, Basilicata, Calabria e Sicilia.
Biologia: detriti di *Artemisia* spp. e *Alnus* spp.

101. ***Stygnocoris pygmaeus*** (Sahlberg, 1848)
Corotipo: E-Europeo (EEU).
Presenza in Italia: Trentino, Alto Adige e Lombardia.
Biologia: detriti di Ericacee, soprattutto *Calluna vulgaris*.

102. ***Pachybrachius fracticollis*** (Schilling, 1829)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali sino all'Emilia; dubbie le citazioni per il Sud.
Biologia: *Carex* spp., *Scirpus* spp., *Verbascum* spp.

103. ***Beosus maritimus*** (Scopoli, 1763)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: detriti di ericacee e poacee.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto in un prato vicino a Camporeso.

104. ***Aellopus atratus*** (Goeze, 1778)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: su *Echium* spp.

105. ***Rhyparochromus quadratus*** (Fabricius, 1758)
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM).
Presenza in Italia: tutte le regioni.
Biologia: detriti di Ericacee.

106. ***Rhyparochromus alboacuminatus*** (Goeze, 1778)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: detriti di Poacee ed Ericacee.
Note di raccolta: l'insetto è stato raccolto in un prato vicino a Camporeso.

107. ***Rhyparochromus confusus*** (Reuter, 1886).
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutte le regioni.
Biologia: detriti di Poacee.

108. ***Rhyparochromus vulgaris*** (Schilling, 1829)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutte le regioni.
Biologia: detriti di Poacee.

109. ***Rhyparochromus phoeniceus*** (Rossi, 1794)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni, tranne la Sardegna.
Biologia: detriti di latifoglie e Poacee.
Note di raccolta: fuori dalle staz. 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo conduce alla Sella della Pila.

110. ***Rhyparochromus pini*** (Linné, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni, tranne la Sardegna.
Biologia: detriti vegetali di Poacee, latifoglie e aghifoglie.

111. ***Peritrechus geniculatus*** (Hahn, 1832)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: regioni settentrionali, Emilia, Toscana, Lazio, Abruzzo, Campania e Sardegna.
Biologia: detriti vegetali di Poacee, Ericacee e altre latifoglie.

112. ***Peritrechus gracilicornis*** Puton, 1877
Corotipo: Turanico-Mediterraneo (TUM).
Presenza in Italia: tutte le regioni, anche se risultano dubbie le citazioni per le due isole maggiori.
Biologia: detriti di Poacee, Ericacee e altre latifoglie.

113. ***Paromius leptopoides*** (Baerenspung, 1859)
Corotipo: Mediterraneo (MED).
Presenza in Italia: tutte le regioni e la Sardegna, tranne la catena alpina.
Biologia: detriti di Poacee.

114. ***Megalonotus praetextatus*** (Herrich - Schaffer, 1835)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: detriti di piante erbacee.

115. ***Megalonotus antennatus*** (Schilling, 1829)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, sino all'Emilia.
Biologia: detriti vegetali, con preferenza di suoli sabbiosi.

116. ***Megalonotus dilatatus*** (Herrich - Schaffer, 1835), Fig. 3
Corotipo: Europeo (EUR).
Presenza in Italia: in letteratura compaiono vecchie citazioni sparse qua e là nelle regioni settentrionali e qualcuna più recente, riferita ad ambienti di brughiera (Dioli, 1980). Segnalato anche nelle regioni meridionali (Faraci & Rizzotti, 1995), ma raro e localizzato ovunque. Primo reperto in Lombardia.
Biologia: detriti di *Sarothamnus* spp. e *Genista* spp.

117. ***Emblethis verbasci*** (Fabricius, 1803)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni
Biologia: fra i detriti di Poacee, Ericacee, felci ecc...

Pyrrhocoridae

118. ***Pyrrhocoris apterus*** (Linnè, 1758)
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM).
Presenza in Italia: tutte le regioni
Biologia: alla base di latifoglie (*Tilia* spp., *Betula* spp.).

Coreidae

119. ***Enoplops scapha*** (Fabricius, 1794)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni peninsulari e Sicilia ma non frequente.
Biologia: *Cirsium* spp., in ambienti soleggiati e asciutti.
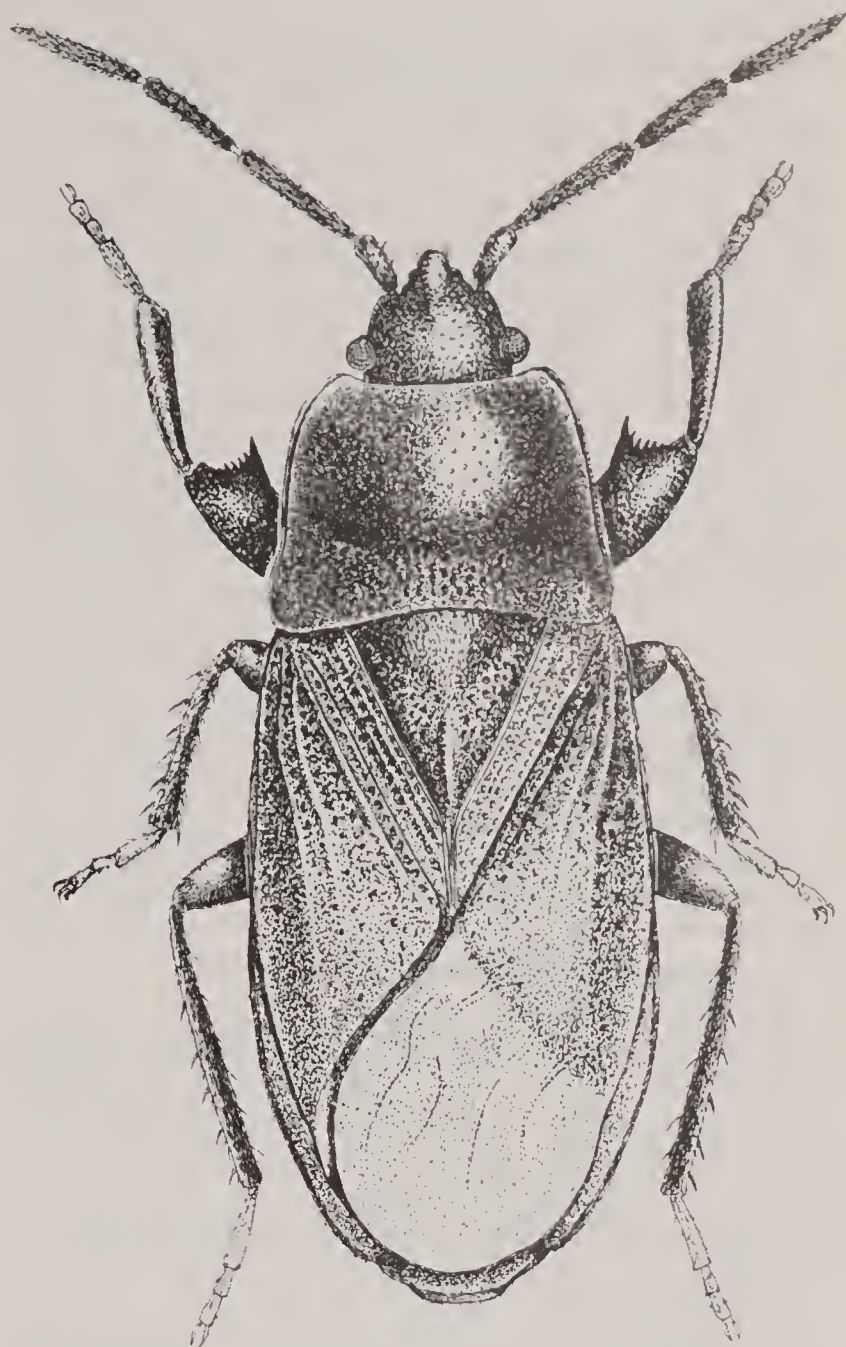
Fig. 3 - *Megalonotus dilatatus* (disegno di C. Pesarini).

120. ***Coreus marginatus*** (Linné, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni, assai comune ovunque.
Biologia: *Rumex* spp.

121. ***Syromastes rhombeus*** (Linné, 1767)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: *Euphorbia* spp. e Cariofillacee (*Spergularia* spp.).

122. ***Gonocerus acuteangulatus*** (Goeze, 1778)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutte le regioni.
Biologia: *Corylus avellana*. In alcune regioni è considerato dannoso alle coltivazioni del nocciolo.

123. ***Spatocera laticornis*** (Schilling, 1829)
Corotipo: Europeo (EUR)
Presenza in Italia: regioni settentrionali alpine.
Biologia: *Polygonum* spp.

124. ***Coriomeris scabricornis*** (Panzer, 1809)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino, Marche, Toscana, Abruzzo, Lazio, Campania, Basilicata, Calabria e Sicilia. Prevalentemente montano.
Biologia: *Trifolium* spp.

125. ***Coriomeris denticulatus*** (Scopoli, 1763)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: su Poacee.

Alydidae
126. ***Alydus calcaratus*** (Linné, 1758)
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni del Nord e del Sud e Sicilia.
Biologia: specie polifaga, le larve si cibano di semi di poacee ma sono state viste anche nutrirsi di carogne o sterco. Esse sono mirmecomorfe e sono state rinvenute spesso con formiche del gruppo «*rufa*», *Lasius* spp. e *Myrmica* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto in un prato vicino a Camporeso.

Rhopalidae
127. ***Corizus hyoscyami*** (Linnè, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: *Verbascum* sp., *Hyoscyamus niger*, *Arthemisia* spp., *Ononis* spp., *Daucus carota*.

128. ***Rhopalus maculatus*** (Fieber, 1837)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: quasi tutte le regioni peninsulari e la Sicilia.
Biologia: ambienti umidi, su *Comarum palustre* e *Cirsium palustre*.

129. ***Rhopalus parumpunctatus*** Schilling, 1829
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: su *Artemisia*, *Achillea*, *Chrysanthemum*, *Eryngium*, *Verbascum*, *Erodium* e *Rumex*.

130. ***Rhopalus conspersus*** (Fieber, 1837)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: su *Thymus*, *Geranium*, *Silene*.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila (m 700) e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

131. ***Rhopalus subrufus*** (Gmelin, 1790)
Corotipo: Cosmopolita (COS).
Presenza in Italia: tutte le regioni, sino a 2.000 metri.
Biologia: su *Trifolium*, *Salvia pratensis*, *Vincetoxicum nigrum*, *Mentha*, *Satureja*, *Urtica*, *Geranium* e *Senecio*.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

132. ***Stictopleurus pictus*** (Fieber, 1861)
Corotipo: Centroasiatico-Mediterraneo (CAM).
Presenza in Italia: tutte le regioni, specie al Sud.
Biologia: *Achillea* e *Artemisia*.

133. ***Stictopleurus abutilon*** (Rossi, 1790)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: *Artemisia*, *Achillea*, *Carlina*, *Chrysanthemum*.

134. ***Stictopleurus crassicornis*** (Linné, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni settentrionali e centrali sino all'Abruzzo.
Biologia: *Artemisia* spp., *Achillea* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo porta alla Sella della Pila e in un prato vicino a Camporeso.

135. ***Stictopleurus punctatonervosus*** (Goeze, 1778)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: *Cirsium*, *Artemisia absinthium*, *Erigeron*.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

Cydnidae
136. ***Sehirus (Tritomegas) bicolor*** (Linné, 1758)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: *Lamium* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto in un prato vicino a Camporeso.

137. ***Sehirus (Adomerus) biguttatus*** (Linné, 1758)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni settentrionali e centrali sino all'Umbria.
Biologia: *Calluna vulgaris*.

138. ***Sehirus (Canthophorus) dubius*** (Scopoli, 1763)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni del Nord e peninsulari.
Biologia: *Thesium* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila (m 700) e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

139. ***Legnotus limbosus*** (Geoffroy, 1785)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Biologia: *Galium* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto presso la vetta.

140. ***Legnotus picipes*** (Fallén, 1807)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni, più raro al Sud dove è specie montana.
Biologia: *Artemisia* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila (m 700) e in un prato della Val Faè vicino alla staz. 7.

141. ***Thyreocoris scarabeoides*** (Linné, 1758)
Corotipo: Europeo-Anatolico (EUR).
Presenza in Italia: regioni centro-settentrionali, più raro al Sud, assente nelle isole.
Biologia: *Potentilla* spp.

Scutelleridae
142. ***Odontotarsus purpureolineatus*** (Rossi, 1790)
Corotipo: Turanico-Mediterraneo (TUM).
Presenza in Italia: tutte le regioni, raro sulle Alpi.

Biologia: *Centaurea* spp., *Cirsium* spp. e *Carduus* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila (m 700) e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

143. ***Eurygaster maurus*** (Linné, 1758)
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM)
Presenza in Italia: tutte le regioni.
Biologia: su poacee.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella della Pila (m 700).

144. ***Eurygaster testudinarius*** (Geoffroy, 1785)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni, non sembra presente sulle isole maggiori.
Biologia: Su Poacee, sino a 1.500 metri di altezza; spesso nei luoghi umidi.

Pentatomidae
145. ***Graphosoma lineatum*** (Linné, 1758)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Biologia: su diverse Apiacee con semi in maturazione.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto presso la vetta e in un prato vicino a Camporeso.

146. ***Podops inuncta*** (Fabricius, 1775)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni italiane, più comune al Nord.
Biologia: detriti di Poacee e Ciperacee, spesso in ambienti semi-paludosi.

147. ***Sciocoris cursitans*** (Fabricius, 1794)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni.
Biologia: nelle praterie secche alla base di *Thymus* spp., *Salvia* spp., *Lotus* spp., *Calluna* spp.

148. ***Sciocoris macrocephalus*** Fieber, 1852
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutte le regioni.
Biologia: alla base di *Thymus* spp., nelle praterie xeriche, spesso lo si trova assieme a *Sciocoris cursitans* (F.).

149. ***Sciocoris homalonotus*** Fieber, 1852
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: regioni settentrionali e Sardegna.
Biologia: *Poa* spp., *Bromus* spp., *Dactylis glomerata*.

150. ***Sciocoris microphthalmus*** Flor, 1860
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali e centrali. Dubbia la presenza di questa specie al Sud e in Sicilia.
Biologia: sotto Ranuncolacee (*Adonis* spp.) e Scrofulariacee (*Rhinanthus* spp.) che sembrano essere le sue piante ospiti.

151. ***Aelia acuminata*** (Linnè, 1758)
Corotipo: Sibirico-Europeo- Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: su Poacee, si comporta da elemento antropofilo legato alle coltivazioni di grano, orzo, segale. Quando queste ultime sono scomparse (come è avvenuto anche sul Barro), la specie si è adattata alle graminacee selvatiche.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto in Val Faè (in un prato vicino alla staz. 7) e in un prato vicino a Camporeso.

152. ***Eysarcoris aeneus*** (Scopoli, 1763)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: su svariate specie di lamiacee.

153. ***Staria lunata*** (Hahn, 1835)
Corotipo: Turanico-Mediterranea (TUM).
Presenza in Italia: in tutte le regioni, ad eccetto della Sardegna, ma sempre in ambienti soleggiati.
Biologia: su *Stachys* spp. e *Lamium* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella d. Pila (m 700), ai margini di un sentiero che dall'eremo porta alla Sella della Pila e in un prato vicino a Camporeso.

154. ***Dryocoris*** (= ***Holcostethus*** Auct.) ***vernalis*** (Wolff, 1804)
Corotipo: Asiatico - Europeo (ASE)
Presenza in Italia: tutte le regioni.
Biologia: su *Verbascum* spp., *Centaurea* spp., *Scrophularia* spp., oltre che su un numero elevato di altre piante ospiti.

155. ***Dryocoris sphacelatus*** (Fabricius, 1794)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, sono degne di verifica le citazioni in Letteratura relative alle regioni a Sud delle Marche.
Biologia: specie polifaga con qualche preferenza per il Verbasco.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei boschi della Val Faè.

156. ***Carpocoris pudicus*** (Poda, 1761)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: in tutte le regioni italiane, tranne la Sardegna.
Biologia: su varie Asteracee.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo porta alla Sella della Pila e in un prato vicino a Camporeso.

157. ***Dolycoris baccarum*** (Linnè, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni, molto comune dal piano sino alle alte quote.
Biologia: specie polifaga su svariate latifoglie.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nel sottobosco della Val Faè e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

158. ***Eurydema ornatum*** (Linnè, 1758)
Corotipo: Centro asiatico-Europeo-Mediterraneo (CEM).

Presenza in Italia: tutte le regioni.
Biologia: fitofago, prevalentemente su brassicacee.

159. ***Eurydema ventrale*** Kolenati, 1846
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni peninsulari e la Sicilia.
Biologia: fitofago, prevalentemente su Brassicacee.

160. ***Eurydema oleraceum*** (Linnè, 1758)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni.
Biologia: su Brassicacee.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto in un prato della Val Faè vicino alla staz. 7 e in un prato vicino a Camporeso.

161. ***Piezodorus lituratus*** (Fabricius, 1794)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni, al Sud è elemento montano.
Biologia: su Fabacee.

162. ***Palomena prasina*** (Linné, 1761)
Corotipo: Sibirico-Europeo-Mediterraneo (SEM).
Presenza in Italia: tutte le regioni.
Biologia: su diverse latifoglie selvatiche o coltivate, con una spiccata predilezione per *Corylus* spp. e *Quercus* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

163. ***Nezara viridula*** (Fabricius, 1775)
Corotipo: Afrotropicale-Indoaustrale-Mediterraneo (AIM).
Presenza in Italia: tutte le regioni centro-meridionali, rara nelle Alpi.
Biologia: specie polifaga, presente soprattutto su brassicacee coltivate ed altre piante ortensi.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto in un prato della Val Faè vicino alla staz. 7.

164. ***Raphigaster nebulosa*** (Poda, 1761)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: vive a spese di larve di Crisomelidi (*Galerucella*) su latifoglie.

165. ***Pentatoma rufipes*** (Linné, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni settentrionali e, con qualche lacuna, in quelle centro meridionali.
Biologia: su *Fagus* spp. e *Alnus* spp.

166. ***Picromerus bidens*** (Linné, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Biologia: su latifoglie, predatore di larve di insetti (soprattutto bruchi di Lepidotteri).

167. ***Zicrona coerulea*** (Linné, 1758)
Corotipo: Olartico (OLA).
Presenza in Italia: tutte le regioni, più comune in quelle centro-meridionali; piuttosto rara sulle Alpi.
Biologia: prevalentemente su *Epilobium* spp. Le larve pare abbiano costumi fitofagi, mentre gli adulti sono predatori di altri insetti.

Acanthosomatidae
168. ***Acanthosoma haemorrhoidale*** (Linné, 1758)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: quasi tutte le regioni peninsulari e Sicilia.
Biologia: su svariate latifoglie, come *Betula, Carpinus, Corylus*. È specie dannosa alle coltivazioni del Nocciolo. In natura, nelle Prealpi, viene collegato con il complesso vegetazionale del «*Querco-Betuletum insubricum*» (Oberdorfer, 1964) (Dioli, 1993).

Plataspidae
169. ***Coptosoma scutellatum*** (Geoffroy, 1785)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni, eccetto la Sardegna.
Biologia: su *Medicago* spp., *Coronilla* spp.
Note di raccolta: fuori dalle stazioni 1-9 l'insetto è stato raccolto nei prati sotto la Sella d. Pila (m 700) e ai margini di un sentiero che dall'eremo porta alla Sella d. Pila.

Considerazioni conclusive

Le specie raccolte sono state raggruppate in base ai corotipi fondamentali della fauna W-paleartica così come enunciati da Vigna & Coll. (1992). In aggiunta viene qui considerato il corotipo «Sibirico-Europeo-Mediterraneo», identificato con la sigla (SEM).

1. Specie ad ampia distribuzione paleartica

(OLA) Olartiche	10
(PAL) Paleartiche	9
(ASE) Asiatiche-Europee	20
(SIE) Sibiriche-Europee	24
(SEM) Sibiriche-Europee-Mediterranee	12
(CEM) Centroasiatiche-Europee-Mediterranee	4
(CAE) Centroasiatiche-Europee	2
(CAM) Centroasiatiche-Mediterranee	2
(TEM) Turaniche-Europee-Mediterranee	21
(TUE) Turaniche-Europee	4
(TUM) Turaniche-Mediterranee	4
(EUM) Europee-Mediterranee	16
TOTALE	128

2. Specie ad ampia distribuzione in Europa

(EUR) Europee	23
(CEU) Centroeuropee	4
(SEU) Sud-Europee	3
(EEU) Est-Europee	1
TOTALE	31

3. Specie ad ampia distribuzione mediterranea

(MED) Mediterranee	6
(EME) E-Mediterranee	1
TOTALE	7

4. Specie afrotropicali e indiane presenti nel Mediterraneo

(AIM) Afrotropicali-Indoaustrali-Mediterranee	1

5. Specie cosmopolite o subcosmopolite

(COS) Cosmopolite	1

6. Specie endemiche italiane

(END)	1

TOTALE COMPLESSIVO	169

In conclusione, la fauna degli eterotteri del Monte Barro risulta notevolmente omogenea con una netta predominanza di specie ad ampia distribuzione come è visualizzato dalla Fig. 4, dove i corotipi sono stati raggruppati per categorie sintetiche.

Tale situazione è determinata dalla presenza di molte specie antropofile, soprattutto tra Miridae, Lygaeidae e Pentatomidae, legate ai coltivi ora degradati. Gli eterotteri appartenenti a questo vasto raggruppamento sono per lo più caratteristici delle steppe a graminacee dell'Europa e dell'Asia media.

Emerge qua e là qualche elemento relitto tipico della brughiera a *Calluna vulgaris*, che rappresenta la componente più preziosa e degna di maggior tutela (*Bothynotus pilosus*, *Megalonotus dilatatus*).

Il Monte Barro, infine, risente climaticamente di una certa «oceanicità», tipica dei territori perilacustri della Lombardia e del Ticino dove si va facendo strada il concetto di fauna «insubrica» (Querco-betuletum insubricum e Corylo-fraxinetum insubricum) (Dioli, 1993) così diversa da quella con caratteristiche sub-mediterranee del Veronese, dei Monti Berici e dei Colli Euganei.

Infatti l'assenza di piante di riferimento, come l'*Erica arborea* ed il *Cistus salvifolius*, inibisce una maggior penetrazione e diffusione delle specie mediterranee xerotermofile.

Per quanto riguarda il confronto fra le stazioni 1-9 in base alle specie che vi sono state rinvenute, utilizzando l'indice di Dice/Sorensen e applicando la cluster analysis secondo il metodo WPGMA si sono ottenuti i dendrogrammi di somiglianza riportati in Fig. 5 e Fig. 6: in uno di essi (fig 5) sono state prese in considerazione tutte le specie raccolte nelle stazioni, nell'altro (Fig. 6) solo quelle esclusivamente o prevalentemente fitofaghe. I due dendrogrammi forniscono gli stessi raggruppamenti a riprova del fatto che le specie predatrici sono sostanzialmente ininfluenti per la caratterizzazione dei biotopi. Diversamente da quanto è stato osservato nei Curculionidi la stazione 9, situata ai margini del lago di Annone, non si stacca da tutte le altre, probabilmente per l'«inquinamento» che le deriva dalla non irrilevante presenza di vegetazione disorganizzata. Si separa invece, in primo luogo, la stazione 6, fisionomicamente ben caratterizzata dalla forte tendenza alla ricostruzione di una foresta moderatamente termofila. Fra le rimanenti stazioni la 7 e la 8, ambedue in Val Faè, occupano una posizione isolata probabilmente per via della loro esposizione fresca.

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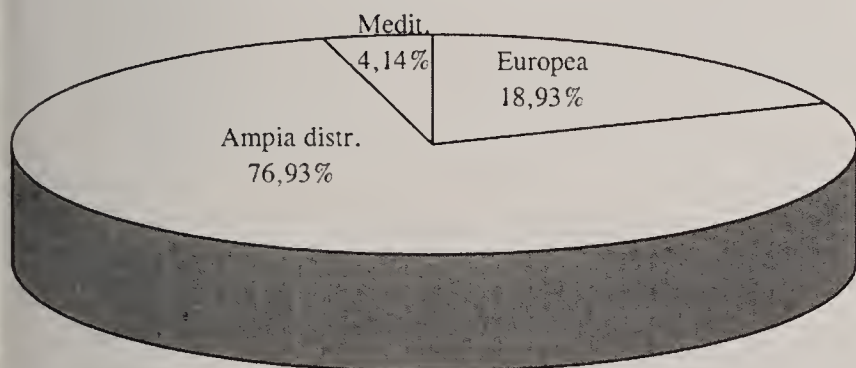
Fig. 4 - Corotipi raggruppati per categorie sintetiche.
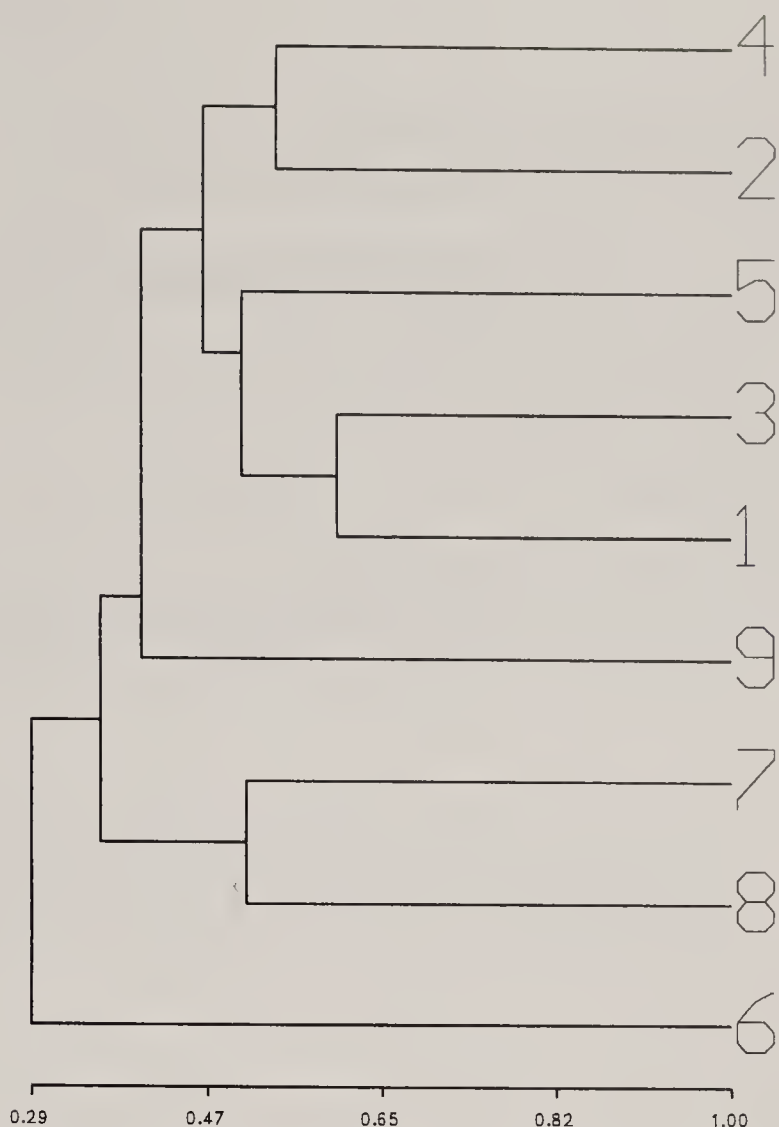
Fig. 5 - Dendrogramma di similarità fra le stazioni 1-9 basato su tutte le specie di Eterotteri presenti nei campionamenti (indice di Dice/Sorensen + WPGMA).
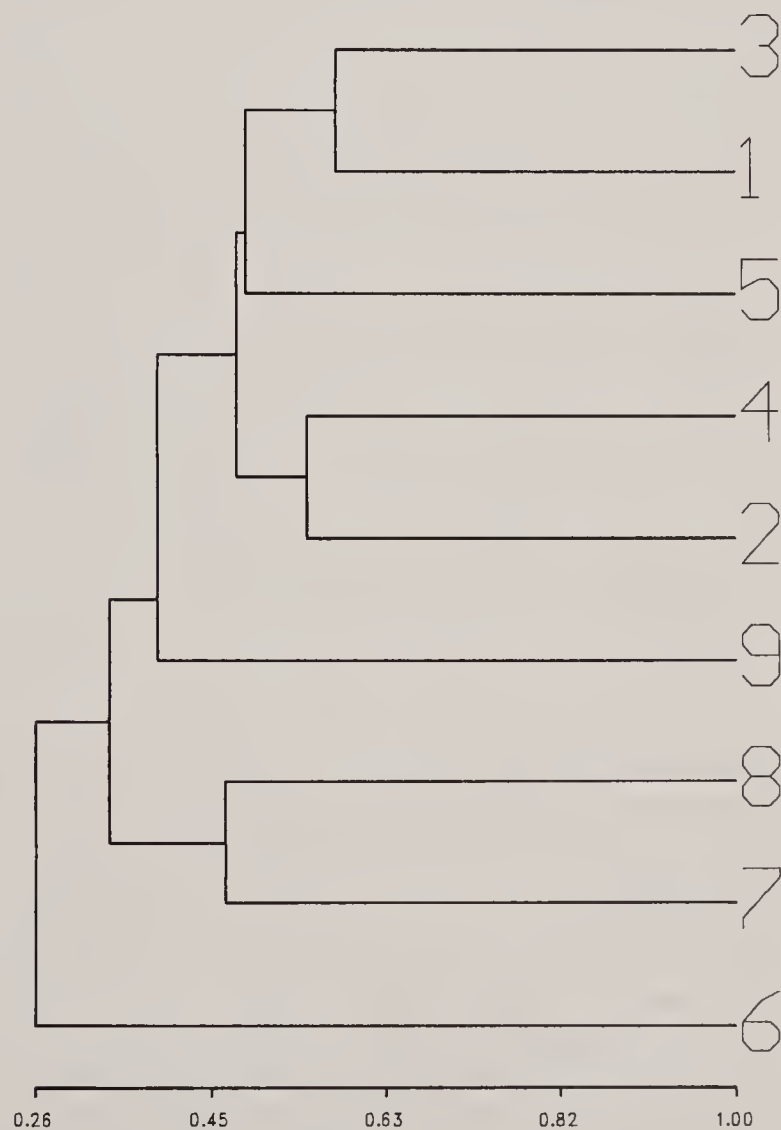
Fig. 6 - Dendrogramma di similarità fra le stazioni 1-9 basato solo sulle specie di Eterotteri che hanno un regime dietetico del tutto o in gran parte fitofago (indice di Dice/Sorensen + WPGMA).

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Gli Elateridi (Coleoptera Elateridae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Questo lavoro contiene una lista di Elateridi presenti nell'area del Monte Barro (Lecco). Il materiale è stato raccolto quasi completamente nell'ambito di una ricerca condotta durante gli anni 1989-1992 dal Museo di Storia Naturale di Milano. Una particolare attenzione è stata rivolta a 9 stazioni prative, di cui si fornisce una breve descrizione. Complessivamente sono state individuate 27 specie di Elateridi, con una netta dominanza di elementi europei o ad ampia distribuzione.

Abstract - Click beetles (Coleoptera Elateridae) from Monte Barro (Italy, Lombardy, Lecco).
In the present paper a list of Elateridae from the area of Monte Barro (Lecco) is given. The material has been almost completely collected during a research accomplished by the Natural History Museum of Milano in the years 1989-1992. Nine sampling sites have been particularly investigated and shortly described. Twenty-seven species have been collected, most of which European or widely distributed in the Palaearctic Region. The number of Mediterranean elements is unimportant, owing to the absence of the typical Mediterranean host plants.

Key words: Monte Barro, Elateridae, geographic distribution.

Negli anni 1989-1992 il Museo civico di Storia Naturale di Milano ha condotto una ricerca entomofaunistica nell'area del Monte Barro (Lombardia, Lecco) col contributo del Consorzio Parco. Per quanto riguarda il popolamento di Coleotteri Elateridi, le ricerche effettuate non hanno fornito un quadro faunistico particolarmente ricco, ma sicuramente significativo, poiché se il numero di specie individuate (27) non è particolarmente elevato, il numero di esemplari campionati è per contro cospicuo; anche se è pressoché certo che l'area indagata ospiti anche altre specie, appare indubbio che, con la presente ricerca, siano state individuate tutte le entità più diffuse e caratteristiche. Dei dati qui forniti, un ristretto numero è da riferirsi a raccolte effettuate prima dell'inizio delle campagne di ricerca dal Dr. Spreafico nei dintorni di Galbiate, quindi ai margini dell'area del Parco, o di poco al difuori dei suoi confini.

Osservazioni sulle stazioni di raccolta

Una parte delle raccolte è stata effettuata in 9 stazioni prative (stazioni 1-9), di cui si riportano le caratteristiche ambientali ricavate dal contributo di Banfi, Galasso & Sassi, in questo stesso volume. Ulteriori stazioni di raccolta sono state riunite, nella tabella riassuntiva (tab. 1), in una sorta di stazione cumulativa indicata con il numero 10.

Stazione 1: Località Piani di Barra, 610 m, esp. W, interessata da scavi archeologici (Grande Edificio). È caratterizzata da una consistente presenza di prato falciabile che indica una attività di foraggio residua.

Stazione 2: Località Piani di Barra, 600 m, esp. W, interessata da scavi archeologici (Edificio II). Si tratta di una prateria in cui è stata abbandonata la gestione a foraggio, vi è quindi presente un leggero mantello.

Stazione 3: Conca prativa a monte del Monumento dell'Alpino, 630 m, esp. W. Vi si nota la convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion* è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. È un prato arido con montarozzi residui a brughiera; per il resto il livello di base è costituito da prateria a *Brachypodium rupestre* ssp. *caespitosum*.

Stazione 6: Superfici prative lungo il sentiero della «Cresta occidentale», che dall'edificio dell'ex sanatorio sale alla vetta, 750 m, esp. S. Si tratta di una prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura, con forte influsso dell'elemento prenemorale (tendenza a un *Quercetum pubescentis* s. l.)

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. È una superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8 ma più aperta e con qualche elemento in più di *Mesobromion*.

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. È un prato terrazzato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili.

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Vi si evidenziano tre aspetti essenziali: 1) il canneto, con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto e residui di bosca-

glia ripariale 2) prato umido oligotrofico (*Molinion coeruleae*); 3) vegetazione erbacea perenne e disorganizzata al margine superiore della stazione.

Elenco delle specie raccolte

Agrypnus murinus (Linneo)
Corotipo: Olartico (OLA).
Presenza in Italia: tutta Italia e Sicilia.
Svariati esemplari raccolti in maggio e giugno nelle staz. 1, 2, 3, 4, 5 e ai margini di un sentiero che dall' eremo porta alla Sella d. Pila.

Drasterius bimaculatus (Rossi)
Corotipo: W-paleartico (WPA).
Presenza in Italia: tutta Italia e isole.
Due esemplari raccolti nella staz. 1 (19.V.1991, lg.Leonardi e 8.VI.1991, lg. Sassi).

Actenicerus sjaelandicus (Müller)
Corotipo: Olartico (OLA).
Presenza in Italia: Italia settentrionale, Toscana.
Un solo esemplare raccolto nella staz. 9 (16.V.1990, lg. Sassi).

Cidnopus pilosus (Leske)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e Sicilia.
Numerosi esemplari raccolti in maggio e giugno nelle staz. 1, 3, 4, 5, 6, 7 e 8, e ai margini di un sentiero che porta dall' eremo alla Sella d. Pila.

Kibunea minuta (Linneo)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia e Sicilia.
Svariati esemplari raccolti in maggio e giugno nella staz. 2, inoltre un esemplare nella staz. 4 (10.VI.1990, lg.Sassi) e un altro nella staz. 5 (24.VI.1992, lg. Sassi).

Limonius quercus (Olivier)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta l'Italia continentale.
Numerosissimi esemplari raccolti in tutte le stazioni (ad eccezione della staz. 9) da maggio a luglio, con maggiore abbondanza in maggio.

Nothodes parvulus (Panzer)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e Sardegna.
Tre esemplari raccolti nella staz. 6 (6.VII.1990, lg. Sassi).

Athous haemorrhoidalis (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta l'Italia continentale.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 2, 3, 4, 6 e 8, altri esemplari provengono dai prati sotto Sella d. Pila, da un prato vicino a Camporeso e dal sottobosco della Val Faè.

Athous vittatus (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e Sicilia.
Numerosi esemplari esemplari raccolti in maggio e giugno nelle staz. 1 e 2.

Athous flavipennis Candèze
Corotipo: Alpino.
Presenza in Italia: Piemonte, Liguria, Lombardia, Trentino e Appennino settentrionale.
Alcuni esemplari raccolti a fine maggio ed in giugno nelle staz. 2, 3, 4 e 5 e ai margini di un sentiero che porta dall' eremo alla Sella della Pila.

Athous bicolor (Goeze)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta l'Italia continentale ad eccezione della Calabria.
Alcuni esemplari raccolti a fine maggio e in giugno nelle staz. 2, 3, 4 e 6.

Hemicrepidius hirtus (Herbst)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia e Sicilia.
Un unico reperto (sentiero che porta dall' eremo alla Sella d. Pila, 6.VII.1990, lg. Sassi).

Adrastus axillaris Erichson
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale, Toscana, Marche, Abruzzo, Basilicata.
Un solo esemplare raccolto nella staz. 2 (27.V.1989, lg. Sassi).

Synaptus filiformis (Fabricius)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia e isole.
Numerosi esemplari raccolti in maggio nella staz. 9.

Agriotes acuminatus (Stephens)
Corotipo: Europeo (EUR).
Presenza in Italia: presente in gran parte dell'Italia continentale.
Un unico reperto (Boschi della Val Faè, 23.V.1991, lg. Sassi).

Agriotes brevis Candèze
Corotipo: Europeo (EUR).
Presenza in Italia: presente in tutta l'Italia continentale.
Alcuni esemplari raccolti in maggio nelle staz. 1, 2 e 3.

Agriotes lineatus (Linneo)
Corotipo: Olartico (OLA).
Presenza in Italia: tutta Italia e isole.
Un unico reperto (staz.9, 25.V.1990, lg. Sassi).

Agriotes litigiosus (Rossi)
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutta Italia e Sicilia.
Alcuni esemplari raccolti in giugno e luglio nelle staz. 4 e 9.

Agriotes ustulatus (Schaller)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale e centrale, Sicilia.
Un unico reperto (staz. 4, 8.VII.1990, lg. Sassi).

Ampedus pomonae (Stephens)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale, Toscana, Puglia.
Un esemplare raccolto nella staz. 9 (16.V.1990, lg. Leonardi).

Ampedus pomorum (Herbst)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta l'Italia continentale.
Un esemplare raccolto nella staz. 9 (25.V.1990, lg. Sassi).

Melanotus crassicollis (Erichson)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e isole.
Due soli reperti (Galbiate, 30.V.1971 e 27.VII.1980, lg. Spreafico).

Melanotus punctolineatus (Pelerin)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e Sicilia.
Alcuni esemplari raccolti in maggio e giugno nella staz. 2, 3 e 6.

Melanotus tenebrosus (Erichson)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e isole.
Numerosi esemplari raccolti nelle staz. 2, 5 e 6 e, sul versante meridionale, nei prati sotto Sella della Pila (m 700).

Cardiophorus gramineus (Scopoli)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Puglia, Calabria.
Un esemplare raccolto a Galbiate 83.V.1970, lg. Spreafico)

Cardiophorus rufipes (Goeze)
Corotipo: Mediterraneo-Europeo (EUM).
Presenza in Italia: tutta Italia e isole.
Un unico reperto (staz. 2, 19.V.1991, lg. Leonardi).

Dicronychus cinereus (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia e Sicilia.
Due soli esemplari raccolti nella staz. 2 a distanza di un anno esatto l'uno dall'altro (15.VI.1989 e 15.VI.1990, lg. Leonardi).

Considerazioni conclusive

Più che per altre famiglie, nel caso degli Elateridi si è potuta osservare una predominanza quantitativa molto accentuata di alcune specie: più della metà degli esemplari raccolti appartenevano ad una specie sola, *Limonius quercus*, e dei rimanenti più della metà appartenevano alle due specie *Athous vittatus* ed *A. haemorrhoidalis*. Per contro, ben 10 delle 27 specie rinvenute sono state raccolte in un unico esemplare. Nettamente predominanti, nel quadro corologico, le specie europee e sibirico-europee, come si ricava dalla tabella 2; è interessante osservare inoltre che le specie europee sono nettamente più numerose di quelle ad ampia distribuzione paleartica, come emerge con maggior evidenza dalla fig. 1, dove i corotipi sono stati raggruppati per categorie sintetiche. Va però rilevato che le specie indicate come europee in base ai corotipi cui ci si è attenuti nel presente contributo sono in molti casi presenti anche in Asia minore, e che per esse la più opportuna definizione del corotipo sarebbe quella, non contemplata, di Euro-Anatolico. Il numero di tali elementi è indicato, fra parentesi, dopo quello globale del corotipo europeo.

Tabella 1 - Tabella riassuntiva delle specie raccolte.

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Agrypnus murinus	+	+	+	+	+					+
Drasterius bimaculatus	+									
Actenicerus sjaelandicus									+	
Cidnopus pilosus	+		+	+	+	+	+	+		+
Kibunea minuta		+		+	+					
Limonius quercus	+	+	+	+	+	+	+	+		+
Nothodes parvulus						+				
Athous haemorrhoidalis		+	+	+		+		+		+
Athous vittatus	+	+								
Athous flavipennis		+	+	+	+					+
Athous bicolor		+	+	+		+				
Hemicrepidius hirtus										+
Adrastus axillaris		+								
Synaptus filiformis									+	
Agriotes acuminatus										+
Agriotes brevis	+	+	+							
Agriotes lineatus									+	
Agriotes litigiosus				+					+	
Agriotes ustulatus				+						
Ampedus pomonae									+	
Ampedus pomorum									+	
Melanotus crassicollis										+
Melanotus punctolineatus		+	+			+				
Melanotus tenebrosus		+			+	+				+
Cardiophorus gramineus										+
Cardiophorus rufipes		+								
Dicronychus cinereus		+								

Tabella 2 - Spettro corologico delle specie raccolte. Le sigle dei corotipi fondamentali sono ricavate dal lavoro di Vigna Taglianti et al. (1992).

Corotipo	n° specie	% sul totale
Europeo (EUR)	13(8)	48,15
Sibirico-Europeo (SIE)	6	22,22
Olartico (OLA)	3	11,11
Europeo-Mediterraneo (EUM)	2	7,41
W-Paleartico (WPA)	1	3,70
S-Europeo (SEU)	1	3,70
Alpino	1	3,70
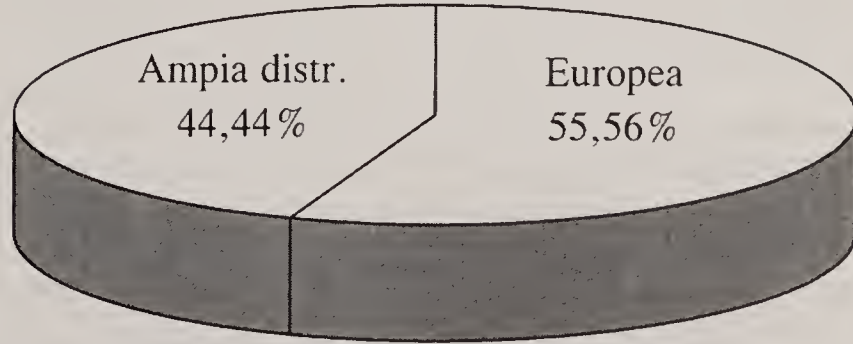
Fig. 1 - Corotipi raggruppati per categorie sintetiche.

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I Coccinellidi (Coleoptera Coccinellidae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - L'autore presenta l'elenco di 23 specie di Coccinellidi raccolti sul rilievo brianteo del Monte Barro. Le raccolte si sono concentrate soprattutto in 9 stazioni prative (staz. 1-9), 8 delle quali situate all'interno del parco regionale. Di ciascuna specie vengono forniti i dati ecologici, corologici ed il numero di esemplari raccolti. Viene rilevata la presenza di una popolazione numerosa ed omogenea di *Scymnus femoralis* (Gyllenhal). Di questa specie viene ridescritta la femmina e vengono fornite le differenze più rilevanti con le specie affini.

Abstract - Ladybird beetles (Coleoptera Coccinellidae) from Monte Barro (Italy, Lombardy, Lecco).
The author gives the list of 23 species of Coccinellidae collected on Monte Barro Regional Park. Nine sampling sites have been particularly investigated, eight of which are placed inside the Regional Park. Ecological, distributional data and the number of specimens collected are given for every species. The presence of a conspicuous and homogeneous population of *Scymnus femoralis* (Gyllenhal) is noticed. The female of that species is redescribed and the most relevant differences with similar species are given.

Key words: Monte Barro, Coccinellidae, geographic distribution.

Il Monte Barro è una piccola elevazione montuosa situata a sud-ovest del ramo orientale del Lago di Como. Ha un'altezza di m 922 ed il suo territorio, per le sue peculiarità botaniche, geografiche e storiche è stato costituito a Parco naturale della Regione Lombardia nel 1983. I suoi aspetti geomorfologici, botanici e storici sono già stati illustrati da Banfi, Galasso & Sassi in questo stesso volume.

I Coccinellidi, sono stati raccolti in varie stazioni negli anni 1989-92, nei mesi da marzo ad ottobre. Sono stati esaminati più di 350 esemplari appartenenti a 23 specie, circa 1/5 della fauna italiana.

Il maggior numero dei sopralluoghi è stato effettuato in 9 stazioni prative (stazioni 1-9) di cui si riportano le caratteristiche ambientali essenziali, ricavate dal contributo di Banfi, Galasso & Sassi.

Stazione 1: Località Piani di Barra, 610 m, esp. W, interessata da scavi archeologici (Grande Edificio). È caratterizzata da una consistente presenza di prato falciabile che indica una attività di foraggio residua.

Stazione 2: Località Piani di Barra, 600 m, esp. W, interessata da scavi archeologici (Edificio II). Si tratta di una prateria in cui è stata abbandonata la gestione a foraggio, vi è quindi presente un leggero mantello.

Stazione 3: Conca prativa a monte del Monumento dell'Alpino, 630 m, esp. W. Vi si nota la convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion* è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. È un prato arido con montarozzi residui a brughiera; per il resto il livello di base è costituito da prateria a *Brachypodium rupestre* ssp. *caespitosum*.

Stazione 6: Superfici prative lungo il sentiero della «Cresta occidentale», che dall'edificio dell'ex sanatorio sale alla vetta, 750 m, esp. S. Si tratta di una prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura, con forte influsso dell'elemento prenemorale (tendenza a un *Quercetum pubescentis* s. l.).

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. È una superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8 ma più aperta e con qualche elemento in più di *Mesobromion*.

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. È un prato terrazzato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili.

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Vi si evidenziano tre aspetti essenziali: 1) il canneto, con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto e residui di boscaglia ripariale 2) prato umido oligotrofico (*Molinion coeruleae*); 3) vegetazione erbacea perenne e disorganizzata al margine superiore della stazione.

Elenco delle specie raccolte

La determinazione degli esemplari è stata fatta in base ai lavori di Mader, Fürsch, Iablokoff- Khnzorian e per conoscenza personale.

I corotipi sono stati attribuiti secondo le indicazioni di Vigna Taglianti et Al. I dati ecologici sono tratti dal «Die Käfer Mitteleuropas-Ökologie», Vol 2, di K.Koch.

Scymnus (Neopullus) haemorrhoidalis (Herbst, 1797)

Stazione: **1**, 10.VI.91, 1 es; **3**, 23.V.91, 1 es; **9**, 15.VI.90, 4 es.

Corotipo: Sibirico-Europeo (SIE).

Distribuzione in Italia: Indicato di tutta Italia (Porta, Luigioni), Sardegna (Luigioni). Comune nell'Italia settentrionale e centrale nelle zone umide e paludose. Più raro ed isolato al sud ove si rinvengono esemplari con il pronoto completamente rosso. Non conosco esemplari di Sicilia e Sardegna.

Dati ecologici: specie euritopa, prevalentemente arboricola, afidofaga. Il suo habitat è costituito da praterie umide, rive di fiumi e ruscelli (soprattutto boschetti di *Salix* e *Alnus*), zone sabbiose e argillose; frequenta sia il fogliame che i vegetali secchi.

Scymnus (s. str.) femoralis (Gyllenhal, 1827) Fig. 1b, 2b, 3b, 4b, 5b

Stazione: **1**, 23.V.91, 1 es; 30.V.91, 1 es; **2**,15.VI.90, 8 es; **3**, 9.V.90, 4 es.; 23.V.91, 1 es; 10.VI.91, 1 es; **4**, 21.III.90, 1 es; 10.VI.91, 2 es; **5**, 16.V.90, 1 es; **6**, 27.VI.89, 2 es; 6.V.90, 2 es.; 22.VI.92, 1 es; 1.VII.92, 1 es; **9**, 15.VI.90, 1 es.

Corotipo: Europeo (EUR).

Distribuzione in Italia: regioni settentrionali e centrali.

Dati ecologici: specie stenotopa, xerofila, erbicola e arbusticola, afidofaga. Il suo habitat è costituito da rive fluviali sabbiose, praterie aride, bordi soleggiati di boschi; frequenta sia il fogliame che i vegetali secchi.

Note sistematiche: la validità di questo taxon è stata messa in dubbio. Descritto da Gyllhenhal come specie a sè, è stato successivamente messo in sinonimia con *Scymnus pygmaeus* (Fourcroy, 1785) (sinonimo di *Sc. rubromaculatus* Goeze, 1777) ed infine di *Scymnus interruptus* (Goeze, 1777). L'apparato genitale maschile è identico a quello di *Sc. interruptus* ma le due forme non convivono. Per esempio in Gran Bretagna è presente solo *Sc. femoralis* e Pope nella sua monografia degli Scymnini delle Isole Britanniche lo considere buona specie. Anche Fürsch (1967:245) lo cita come specie a sè stante. Mentre i maschi sono facilmente classificabili per la colorazione e l'apparato genitale, le femmine sono difficilmente distinguibili da quelle di *Sc. rubromaculatus*. Fürsch indica come carattere distintivo la morfologia delle clave antennali, strette e fusiformi in *Sc. rubromaculatus*, larghe e ad estremità ingrossata in femoralis. La presenza sul Monte Barro di una popolazione omogenea di *Sc. femoralis* mi ha dato l'occasione di esaminare un certo numero di femmine appartenenti con sicurezza a tale specie e di fornire alcuni caratteri differenziali con le altre specie di *Scymnus (s. str.)* e *Scymnus (Pullus)* che hanno caratteristiche di colorazione e morfolgia esterna molto simili: *Scymnus rubromaculatus*, *Scymnus (Pullus) auritus* e *Scymnus (Pullus) fraxini* (Figg. 1-4).

La femmine di *Sc. femoralis* è caratterizzata da uno stretto orlo marginale anteriore del pronoto rossastro, in *Sc. rubromaculatus* l'orlo anteriore rossastro è generalmente più esteso e gli angoli anteriori del pronoto sono anch'essi rossi mentre in *Sc. femoralis* sono sempre neri. Il receptaculum seminis in *Sc. femoralis* ha il nodulus lievemente più allungato che in *Sc. rubromaculatus*. Non ho trovato differenze importanti nella larghezza della clava antennale che sembra, al contrario di quanto affermato da Fürsch, più larga in *Sc. rubromaculatus*. Anche la colorazione nera dei femori in *Sc. femoralis* non è un carattere sicuro poichè si trovano spesso esemplari di *Sc. rubromaculatus*, specialmente femmine, con femori medi e posteriori anneriti. *Scymnus (Pullus) auritus* si distingue facilmente per avere gli ultimi sterniti addominali rossi, le linee metacoxali complete, la punteggiatura del pronoto spesso indistinta, evanescente. *Scymnus (Pullus) fraxini* è di dimensioni minori, forma del corpo più stretta, punteggiatura elitrale più robusta, macchia del pronoto della femmina molto caratteristica. La colorazione, come in tutti i Coccinellidi, può variare, ma generalmente i caratteri sopra descritti sono abbastanza costanti. Le differenze tra le singole specie sono riassunte nella tabella 1.

Scymnus (s. str.) frontalis (Fabricius, 1787)

Stazione: **1**, 10.VI.91, 1 es; **2**, 15.VI.89, 1 es; 2.VI.92, 1 es; **3**, 9.V.90, 3 es.; 10.VI.91, 1 es; 10.X.91, 1 es; **4**, 27.VI.89 1 es; 30.III.90, 1 es; 23.V.91, 3 es; 10.VI.91, 4 es; 1.VII.92, 1 es; **5**, 10.VI.91, 1 es.; **6**, 27.VI.89, 4 es; 1.VII.92, 1 es ; **9**, 15.VI.90, 33 es; 20.VII.90, 1 es; altre, 16.V.90, 1 es.; 13.IX.90, 1 es.
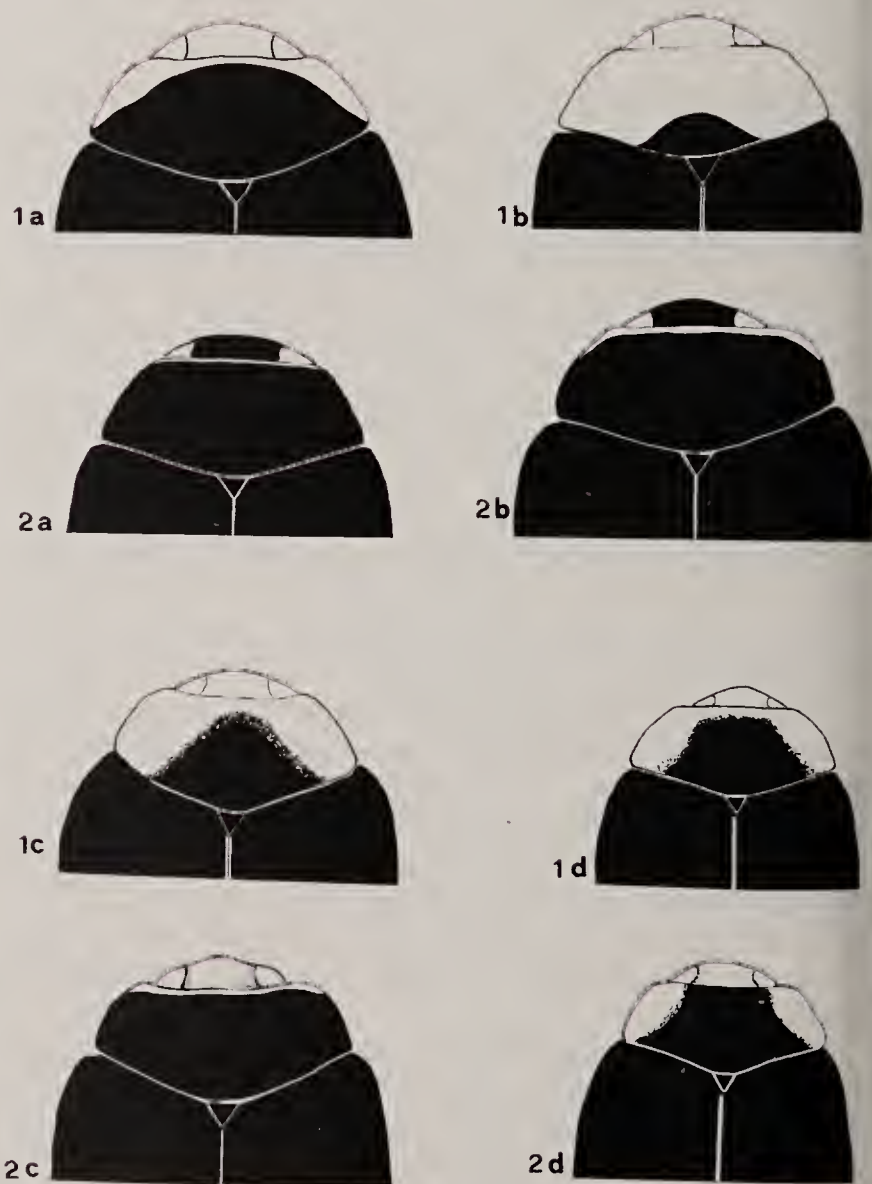
Fig. 1-2 - Pronoto del ♂ (1) e pronoto della ♀ (2) di: a) *Sc. femoralis*; b) *Sc. rubromaculatus*; c) *Sc. auritus*; d) *Sc. fraxini*.
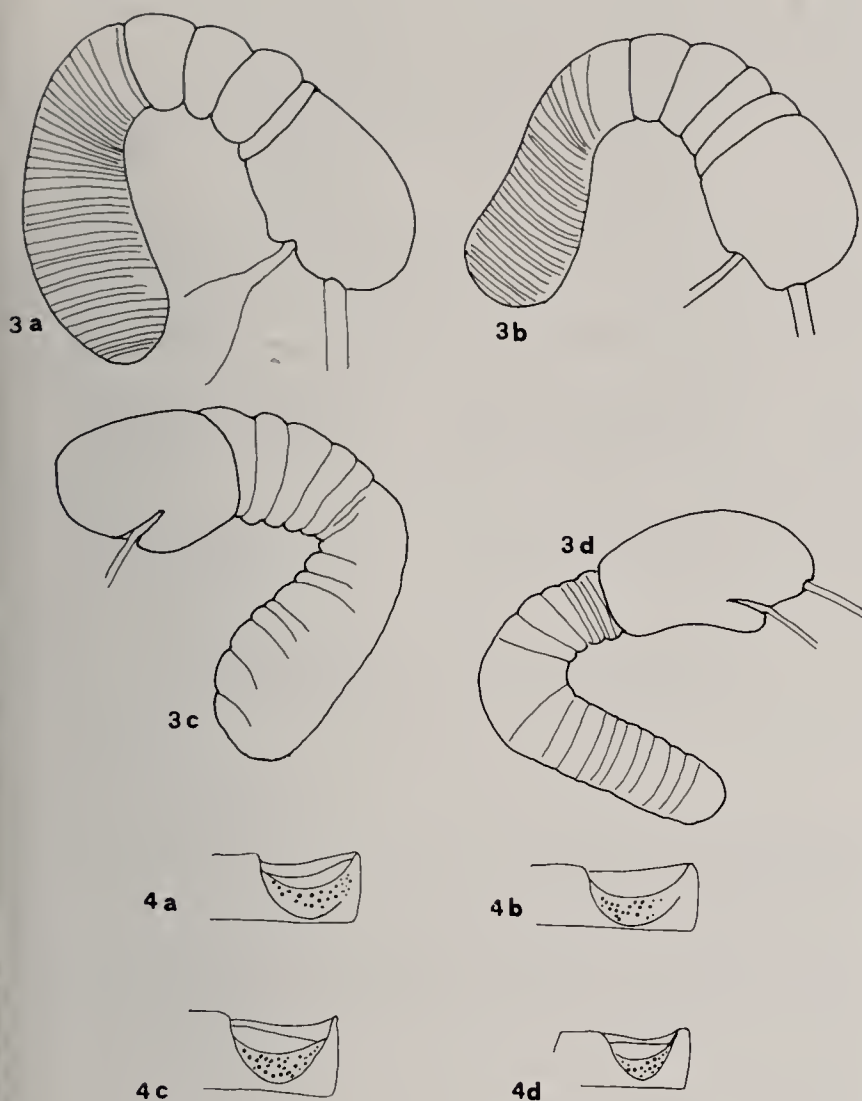
Fig. 3-4 - *Receptaculum seminis* (3) e linee metacoxali (4) di: a) *Sc. femoralis*; b) *Sc. rubromaculatus*; c) *Sc. auritus*; d) *Sc. fraxini*.
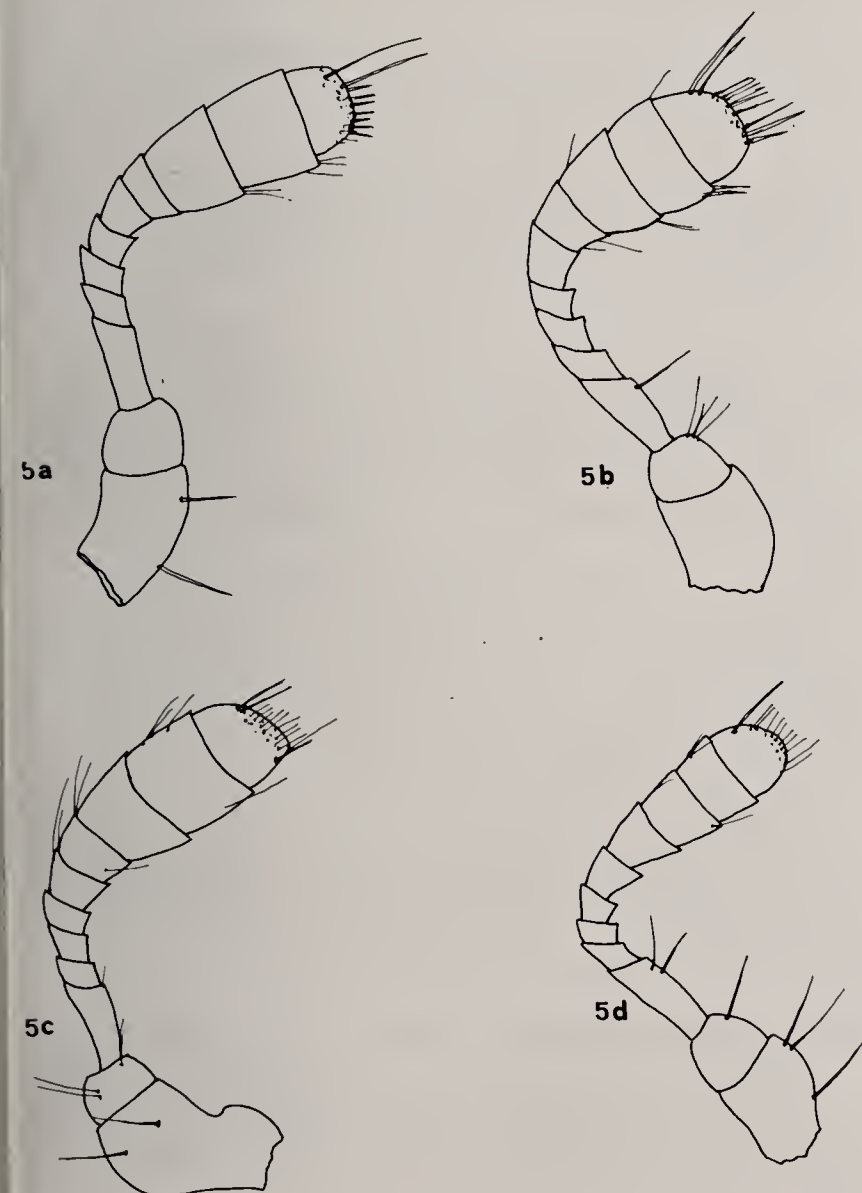
Fig. 5 - Antenna di: a) *Sc. femoralis*; b) *Sc. rubromaculatus*; c) *Sc. auritus*; d) *Sc. fraxini*.

Corotipo: Centroasiatico-Europeo (CAE).

Distribuzione in Italia: tutta la penisola, sostituito nelle regioni meridionali dalla forma *immaculatus* Suffrian. Manca in Sicilia, Sardegna ed isole minori.

Dati ecologici: specie euritopa, xerofila, erbicola e arbusticola, afidofaga. Il suo habitat è costituito da praterie soleggiate e margini di boschi.

Scymnus (s. str.) pallipediformis apetzoides Capra & Fürsch, 1967

Stazione: **1**, 10.X.91, 1 es; **2**, 15.VI.89, 1 es; 15.VI.90, 2 es; 19.V.91, 1 es; **3**, 20.IX.89, 1 es; 10.X.91, 1 es; **4**, 27.VI.89, 1 es; 23.V.91, 1 es; 10.VI.91, 1 es; **5**, 16.V.90, 4 es; 10.VI.91, 2 es; **6**, 27.VI.89, 5 es; 1.VII.92, 1 es; **8**, 25.VIII.92, 1 es.

Corotipo: Turanico-Europeo (TUE).

Distribuzione in Italia: regioni settentrionali e centrali sino al Molise ed Altipiano del Matese.

Dati ecologici: specie stenotopa, termofila (frequenta ambienti caldi e soleggiati), erbicola e arbusticola, afidofaga.

Note sistematiche: descritto dapprima come specie a sè, è stato in seguito riconosciuto come sottospecie di *Sc. pallipediformis* dell'Asia Minore. La forma tipica ha due macchie elitrali, mentre la sottospecie *apetzoides* presenta una macchia per ciascuna elitra. È molto simile a *Sc. apetzi* Muls. da cui si distingue oltre che per l'apparato genitale maschile, anche per il colore leggermente più chiaro delle tibie.
Sc. pallipediformis apetzoides popola le aree xerotermiche centro europee ed in Italia si rinviene assieme a *Sc. apetzi* che è più comune. Sul Monte Barro si trova invece soltanto *Sc. pallipediformis apetzoides*.

Nephus (Sidis) anomus Mulsant, 1856

Stazione: **5**, 24.VI.90, 1 es.

Corotipo: Sud-Europeo (SEU).

Distribuzione in Italia: tutta la penisola ed isole ma non comune.

Dati ecologici: specie stenotopa, termofila, afidofaga. Il suo habitat è costituito da praterie soleggiate e margini di boschi; si trova su varie essenze erbacee e nei detriti.

Stethorus punctillum (Weise, 1891)

Stazione: **9**, 16.V.90, 1 es.

Corotipo: Europeo (EUR).

Distribuzione in Italia: tutta la penisola ed isole.

Dati ecologici: specie euritopa, spesso arboricola, tetranicofaga. Frequenta margini di boschi, parchi e giardini, rive di fiumi e torrenti, etc.; si può trovare su *Prunus spinosa* e su varie piante erbacee, meno frequentemente su *Tilia*, *Hedera helix* e nei boschi di conifere.

Platynaspis luteorubra (Goeze, 1777)

Stazione: **2**, 15.VI.89, 1 es; 9.V.90, 1 es; **4**, 27.VI.89, 1 es; 15.VII.91, 1 es.

Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM).

Distribuzione in Italia: tutta Italia.

Dati ecologici: specie euritopa, afidofaga. Si trova generalmente in zone calde, umide o secche, spesso sulle rive di fiumi o torrenti, probabilmente in associazione con formiche del genere *Lasius*. Frequenta varie piante erbacee, arbusti, alberi (*Populus*, *Salix*, *Platanus*, ecc.) e muschi.

Tabella 1 - Caratteri differenziali fra *Scymnus femoralis, Sc. rubromaculatus, Sc. auritus e Sc. fraxini.*

	femoralis	rubromaculatus	auritus	fraxini
punteggiatura pronoto	regolare, piuttosto superficiale, distanza interpunto 2-3 x Ø	regolare, superficiale, distanza interpunto 2-3 x Ø	molto superficiale e fumata, distanza interpunto 3-5 x Ø	regolare, superficiale, distanza interpunto 1-2 x Ø
ultimo sternite addominale	nero	nero	rosso	rosso
articoli clava antennale	stretti, allungati	larghi, corti	stretti, allungati	stretti, corti
pronoto maschio	nero con margini laterali rossi	rosso con macchia semicircolare nera di dimensioni variabili	rosso con macchia semicircolare nera di dimensioni variabili	Rosso con grande macchia trapezoidale nera
pronoto femmina	nero con orlo anteriore rosso molto stretto	nero con angoli e orlo anteriori rossi	nero con angoli e orlo anteriori rossi	nero con lati e ampio orlo anteriore rossi
capo femmina	nero	nero	rosso	rosso
linee metacoxali	complete	complete	incomplete	incomplete

Coccidula rufa (Herbst, 1783)
Stazione: **9**, 21.III.90, 1 es; 6.V.90, 1 es; 9.V.90, 2 es; 19.V.90, 2 es; 16.V.90, 7 es; 25.V.90, 3 es; 15.VI.90, 4 es.
Corotipo: Sibirico-Europeo (SIE).
Distribuzione in Italia: Tutta la penisola, non segnalata di Sicilia; dubbia la presenza in Sardegna.
Dati ecologici: specie euritopa, erbicola e fitodetriticola, afidofaga. Vive in zone paludose e soprattutto nei canneti.

Coccidula scutellata (Herbst, 1783)
Stazione: **9**, 21.IV.92, 2 es.
Corotipo: Sibirico-Europeo (SIE).
Distribuzione in Italia: tutta la penisola ed isole.
Dati ecologici: specie stenotopa, paludicola, erbicola, afidofaga. Si trova su vegetali acquatici e ripicoli, specialmente *Typha* e *Phragmites*.

Anisosticta novemdecimpunctata (Linnaeus, 1758)
Stazione: **9**, 30.III.90, 2 es; 16.V.90, 2 es; 25.V.90, 2 es; 15.VI.90, 7 es.
Corotipo: Sibirico-Europeo (SIE).
Distribuzione in Italia: tutta la penisola, Sicilia; manca in Sardegna.
Dati ecologici: specie stenotopa, paludicola, erbicola, afidofaga. Si trova su vegetali acquatici e ripicoli (*Phragmites, Carex, Glyceria, Salix*) e in detriti.

Hippodamia (s. str.) tredecimpunctata (Linnaeus, 1758)
Stazione: **9**, 30.III.90, 1 es; 15.VI.90, 1 es; 10.X.90, 1 es. 21.IV.92, 1 es.
Corotipo: Olartico (OLA).
Distribuzione in Italia: regioni settenntrionali e centrali, Campania, Sicilia.
Dati ecologici: Specie stenotopa, erbicola, afidofaga. Si trova in ambienti umidi e paludosi, su vegetali ripicoli (specialmente *Carex, Sparganium, Phragmites, Salix*) e in detriti.

Hippodamia (Adonia) variegata (Goeze, 1777)
Stazione: **6**, 6.V.90, 1 es; altre, 30.IX.90, 1 es; 21.IV.92, 1 es.
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM), E-Africano.
Distribuzione in Italia: tutta Italia.
Dati ecologici: specie euritopa, erbicola ed arboricola, afidofaga, comune su varie specie vegetali in zone umide o secche, sia prative che boscate.

Aphidecta obliterata (Linnaeus, 1758)
Stazione: **3**, 9.V.90, 1 es.
Corotipo: Europeo (EUR).
Distribuzione in Italia: Italia settentrionale, Toscana, Lazio, Abruzzo, Calabria.
Dati ecologici: specie euritopa, abitualmente silvicola, arboricola, afidofaga. Si trova di preferenza su conifere dei generi *Pinus* e *Picea*.

Adalia (s. str.) bipunctata (Linnaeus, 1758)
Stazione: **4**, 10.VI.90, 1 es; **9**, 30.III.90, 1 es; 15.VI.90, 1 es; 6.VII.91, 2 es.
Corotipo: Paleartico (PAL), importato in Nord e Sud America.
Distribuzione in Italia: tutta la penisola ed isole.
Dati ecologici: specie ubiquitaria, arboricola ed erbicola, afidofaga.

Adalia (s. str.) decempunctata (Linnaeus, 1758)
Stazione: **1**, 18.VI.91, 1 es; 5.X.94, 1 es; **2**, 15.VI.90, 2 es; **3**, 30.V.90, 1 es; 15.VI.90, 1 es; **4**, 27.VI.89, 1 es; 10.VI.90, 1 es; 24.VI.90, 1 es; **5**, 8.VII.90, 2 es; **6**, 27.VI.89, 1 es; **altre**, 30.V.90, 1 es.
Corotipo: Paleartico (PAL).
Distribuzione in Italia: tutta la penisola ed isole.
Dati ecologici: specie euritopa, talora silvicola, afidofaga. Più arboricola della specie precedente, si trova in genere su noccioli, querce e salici.

Tytthaspis sedecimpunctata (Linnaeus, 1761)
Stazione: **1**, 19.V.91, 5 es; 23.V.91, 1 es; 30.V.91, 1 es; **3**, 10.VI.91, 1 es; **4**, 10.X.90, 2 es; **5**, 10.VI.91, 1 es; **9**, 15.VI.90, 1 es; 6.VII.90, 1 es; **altre**, 6.V.90, 1 es; 23.V.91, 1 es.
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM)

Distribuzione in Italia: tutta la penisola e le isole.
Dati ecologici: specie euritopa, afidofaga. Si trova soprattutto in ambienti sabbiosi e paludosi, sulla vegetazione erbacea e, talora, nei detriti.

Coccinella septempunctata Linnaeus, 1758
Stazione: **1**, 30.V.91, 2 es; **2**, 9.V.90, 3 es; 15.VI.90, 1 es; **3**, 14.III.90, 3 es; 9.V.90, 1 es; **4**, 10.VI.90,1 es; 10.VI.91, 3 es; **5**, 16.V.90, 1 es; 10.VI.90, 1 es; **6**, 9.V.90, 1 es; **altre**, 6.V.90, 1 es; 30.V.90, 2 es; 6.VII.90, 1 es.
Corotipo: Paleartico (PAL), importato in Nord America.Distribuzione in Italia: tutta la penisola e le isole.
Dati ecologici: specie ubiquitaria, erbicola e arboricola, afidofaga.

Oenopia lyncea agnata (Rosenhauer, 1847)
Stazione: **4**, 30.III.90, 1 es; 10.VI.90, 1 es; **8**, 21.IV.92, 1 es.
Corotipo: Centroeuropeo (CEU).
Distribuzione in Italia: regioni settentrionali e zone montuose dell'Italia mediterranea ed isole.
Dati ecologici: specie stenotopa, termofila, arboricola, afidofaga. Il suo habitat abituale è rappresentato da boschi soleggiati di querce; oltre che su *Quercus* a foglie caduche è stata segnalata su *Prunus spinosa*.

Halyzia sedecimguttata (Linnaeus, 1758)
Stazione: **2**, 15.VI.90, 1 es; **3**, 9.V.90, 3 es; 30.V.90, 2 es; **6**, 27.VI.89, 2 es; **8**, 14.III.90, 3 es; **altre**, 9.V.90, 1 es; 21.IV.92, 1 es.
Corotipo: Sibirico-Europeo (SIE).
Distribuzione in Italia: tutta Italia, Sicilia, Sardegna
Dati ecologici: specie stenotopa, silvicola, arboricola, micetofaga; si trova soprattutto su *Quercus, Corylus, Fraxinus, Alnus*; più raramente su *Picea, Pinus, Larix*.

Calvia (Anisocalvia) quatuordecimguttata (Linnaeus, 1758)
Stazione: **3**, 9.V.90, 1 es; 13.IX.90, 1 es; **8**, 14.III.90, 1 es.; **9**, 15.VI.90, 1 es.
Corotipo: Olartico (OLA)
Distribuzione in Italia: Tutta Italia, Sardegna. Sembra mancare in Sicilia.
Dati ecologici: specie euritopa, silvicola, arboricola, afidofaga. Si trova su cespugli ed alberi vari: *Fagus, Quercus, Betula, Alnus, Salix, Fraxinus*, etc.

Propylea quatuordecimpunctata (Linnaeus, 1758)
Stazione: **1**, 30.V.91, 1 es; **3**, 9.V.90, 2 es; 19.V.91, 1 es; ;**4**, 10.VI.90, 2 es; **5**, 16.V.90, 1 es; 10.VI.90, 1 es; 8.VII.90, 2 es; **7**, 9.V.90,1 es; **8**, 16.V.90, 1 es; 6.VII.90, 1 es; **9**, 9.V.90, 1 es; 25.V.90, 1 es; 15.VI.90, 2 es; **altre**, 25.IV.90, 2 es.
Corotipo: Paleartico (PAL), importata in Nord America.
Distribuzione in Italia: tutta la penisola ed isole.
Dati ecologici: specie ubiquitaria, erbicola e arboricola, afidofaga.

Psyllobora vigintiduopunctata (Linnaeus, 1758)
Stazione: **1**, 19.V.91, 1 es; 12.VII.91, 1 es; **2**, 9.V.90, 3 es; 15.VI.90, 1 es; **3**, 9.V.90, 4 es; 13.IX.90, 1 es; **4**, 21.III.90, 1 es; 16.V.90, 1 es; 10.VI.90, 1 es; 24.VI.90, 1 es; 27.VI.90, 1 es; 8.VII.90, 1 es; 13.IX.90, 1 es; **5**, 30.III.90, 1 es; 16.V.90, 1 es; 13.IX.90, 1 es; **6**, 6.VII.90, 1 es; **7**, 16.V.90, 9 es; **8**, 16.V.90, 1 es; **9**, 25.V.90, 1 es; 15.VI.90, 1 es; **altre**, 25.IV.90, 1 es; 6.V.90, 3 es; 9.V.90, 1 es; 16.V.90, 1 es.; 30.V.90, 2 es; 21.IV.92, 2 es.
Corotipo: Paleartico (PAL).
Distribuzione in Italia: tutta la penisola ed isole.
Dati ecologici: specie euritopa, spesso xerofila, erbicola, micetofaga. Il suo habitat è rappresentato da rive di corsi d'acqua o prati asciutti, prati semi umidi, pendii asciutti e caldi, argini e pendii soleggiati, filari di viti, cave, ambienti sabbiosi o ghiaiosi.

Subcoccinella vigintiquatuorpunctata (Linnaeus, 1758)
Stazione: **1**, 23.V.91, 2 es; 10.X.91, 1 es; **2**, 14.III.90, 1 es; 9.V.90, 5 es; 15.VI.90, 2 es; 19.V.91, 2 es; **3**, 20.IX.89, 1 es; **4**, 27.VI.90, 1 es; 20.IX.89, 1 es ; 10.VI.90, 4 es; 24.VI.90, 1 es; 23.V.91, 2 es; **5**, 30.III.90, 2 es; 16.V.90, 2 es; **9**, 30.III.90, 1 es; 9.V.90, 6 es; 16.V.90, 2 es; 16.V.91, 1 es; 15.VI.90, 2 es; 6.VII.90, 4 es; **7**, 25.IV.90, 3 es.; **altre**: 16.V.90, 1 es.
Corotipo: Paleartico (PAL).
Distribuzione in Italia: tutta la penisola e isole.
Dati ecologici: specie euritopa, erbicola, fitofaga. Si trova soprattutto in prati asciutti, campi arati, sponde e pendii, praterie aride. È un insetto polifago rinvenibile su *Medicago, Trifolium, Beta*, e su Cariofillacee (*Saponaria, Silene, Lychnis, Dianthus*)

Tabella 2: tabella riassuntiva delle specie raccolte. Altre stazioni *.

	1	2	3	4	5	6	7	8	9	*
S. haemorrhoidalis	•		•						•	
S. femoralis	•	•	•	•	•	•			•	
S. frontalis	•	•	•	•	•	•			•	•
S. pallipediformis apetzoides	•	•	•	•	•	•		•		•
Nephus anomus					•					
Stethorus punctillum									•	
Platynaspis luteorubra		•		•						
Coccidula rufa									•	
Coccidula scutellata									•	
Anis. novemdecimpunctata									•	
Hippodamia tredecimpunctata									•	
Hippodamia variegata						•				•
Aphidecta obliterata			•							
Adalia bipunctata				•					•	
Adalia decempunctata	•	•	•	•	•	•				•
Tytthaspis sedecimpunctata	•		•	•	•				•	•
Coccinella septempunctata	•	•	•	•	•				•	•
Oenopia lyncea agnata				•				•		
Halyzia sedecimguttata		•	•			•		•		•
Calvia quatuordecimguttata			•					•	•	
Propylea quatuordecimpunct.	•		•	•	•		•	•	•	•
Psyllobora vigintiduopunctata	•	•	•	•	•	•	•	•	•	•
Subco. vigintiquatuorpunctata	•	•	•	•	•		•		•	•

Considerazioni conclusive

Il quadro corologico della popolazione dei Coccinellidi del Monte Barro, come si vede dalla tab.3 e dalla fig. 6, dove i corotipi sono stati raggruppati per categorie sintetiche, mette in evidenza una netta predominanza di specie ad ampia diffusione, che si estende talora a tutta la regione paleartica od olartica, mentre è del tutto assente la componente mediterranea. Solo un elemento, *Nephus* (*Sidis*) *anomus* presenta una diffusione sud europea. Di questa specie, che non figura nel catalogo del «Die Käfer Mitteleuropas», mi era già noto un esemplare del Canton Ticino; la zona prealpina costituisce quindi il suo limite di diffusione settentrionale. È di notevole interesse faunistico la popolazione di *Scymnus* (*s.str.*) *femoralis* in assenza della sua specie più prossima *Sc.* (*s.str.*) *interruptus*. Tale dato sembra avvalorare l'ipotesi che *Sc. femoralis* debba esere considerato una buona specie o per lo meno una razza ecologica. Altro elemento interessante è *Scymnus (s.str.) pallipediformis apetzoides* che forma una popolazione piuttosto abbondante sul Monte Barro, dove non si rinviene invece *Sc. (s.str.) apetzi* che è la specie di *Scymnus* più comune nell'Italia mediterranea. Popolazioni abbondanti di *Sc. pallipediformis apetzoides* sembrano esistere anche nel Canton ticino, infatti ho esaminato numerosi esemplari di questa specie raccolti a Chiasso. Si ha dunque l'impressione che *Sc. pallipediformis apetzoides* sia particolarmente frequente nelle zone calde e soleggiate delle Prealpi.

Tabella 3: spettro corologico delle specie raccolte. Le sigle dei corotipi fondamentali sono ricavate dal lavoro di Vigna Taglianti et al. (1991).

Corotipo	n° specie	% sul totale
Paleartico (PAL)	6	26,09
Sibirico-Europeo (SIE)	5	21,74
Europeo (EUR)	3	13,04
Centroas.-Europeo-Meditt. (CEM)	3	13,04
Olartico (OLA)	2	8,70
Centroasiatico-Europeo (CAE)	1	4,35
Turanico-Europeo (TUE)	1	4,35
S-Europeo (SEU)	1	4,35
Centroeuropeo (CEU)	1	4,35
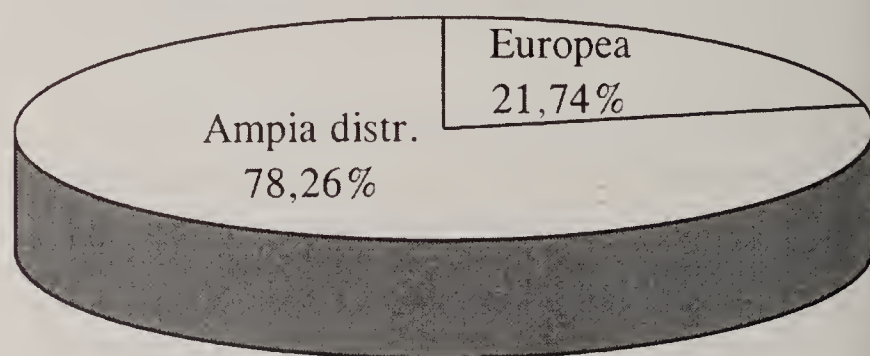
Fig. 6 - Corotipi raggruppati per categorie sistematiche.

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I Cerambicidi (Coleoptera Cerambycidae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Nel presente lavoro viene fornito un elenco delle specie di Cerambicidi rinvenuti nell'area del Monte Barro, come risultato di una ricerca condotta negli anni 1989-1992 dal Museo di Storia Naturale di Milano. Le raccolte sono state effettuate prevalentemente in 9 stazioni prative. Sono state rinvenute 27 specie; una di esse, *Exocentrus lusitanus*, risulta nuova per la fauna lombarda. Viene infine fornita una tabella da cui possono desumersi le caratteristiche biogeografiche della popolazione di Cerambicidi del Monte Barro.

Abstract - Long-horned beetles (Coleoptera Cerambycidae) from Monte Barro (Italy, Lombardy, Lecco).
In the present paper are listed the species of Cerambycidae found in the area of Monte Barro within the framework of a research accomplished by the Natural History Museum of Milano in the years 1989-1992. Mainly nine meadows (sampling sites 1-9) have been investigated. Twenty-seven species have been collected; one of them, *Exocentrus lusitanus*, was not yet known for the Lombard fauna. A brief account on the biogeograpghic pattern of the cerambycid-fauna of Monte Barro is finally given.

Key words: Monte Barro, Cerambycidae, geographic distribution.

Negli anni 1989-1992 il Museo Civico di Storia Naturale di Milano ha condotto una ricerca entomofaunistica nell'area del Monte Barro (Lombardia, Lecco) col contributo del Consorzio Parco. Per quanto riguarda la famiglia *Cerambycidae*, la quantità complessiva di materiale raccolto nel corso di questa ricerca risulta indubbiamente modesta; il numero di specie rinvenute, peraltro, non è del tutto trascurabile, ed il quadro faunistico che ne deriva, pur se indubbiamente incompleto, è comunque significativo, tanto da includere anche una specie che, a dispetto della grande abbondanza di dati esistenti in letteratura sulla famiglia, risulta nuova per la fauna lombarda. Si è pertanto ritenuto opportuno includere anche i Cerambicidi fra le famiglie prese in considerazione nel presente repertorio.

Osservazioni sulle stazioni di raccolta

Una parte delle raccolte è stata effettuata in 9 stazioni prative (stazioni 1-9), di cui riportiamo le caratteristiche ambientali ricavandole dal contributo di Banfi, Galasso & Sassi, in questo stesso volume. Ulteriori stazioni di raccolta sono state riunite, nella tabella riassuntiva (tab. 1), in una sorta di stazione cumulativa indicata con il numero 10.

Stazione 1: Località Piani di Barra, 610 m, esp. W, interessata da scavi archeologici (Grande Edificio). È caratterizzata da una consistente presenza di prato falciabile che indica una attività di foraggio residua.

Stazione 2: Località Piani di Barra, 600 m, esp. W, interessata da scavi archeologici (Edificio II). Si tratta di una prateria in cui è stata abbandonata la gestione a foraggio, vi è quindi presente un leggero mantello.

Stazione 3: Conca prativa a monte del Monumento dell'Alpino, 630 m, esp. W. Vi si nota la convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion* è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. È un prato arido con montarozzi residui a brughiera; per il resto il livello di base è costituito da prateria a *Brachypodium rupestre* ssp. *caespitosum*.

Stazione 6: Superfici prative lungo il sentiero della "Cresta occidentale", che dall'edificio dell'ex sanatorio sale alla vetta, 750 m, esp. S. Si tratta di una prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura, con forte influsso dell'elemento prenemorale (tendenza a un *Quercetum pubescentis* s. l.)

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. È una superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8 ma più aperta e con qualche elemento in più di *Mesobromion*.

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. È un prato terrazzato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili.

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di An-

none. Vi si evidenziano tre aspetti essenziali: 1) il canneto, con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto e residui di boscaglia ripariale 2) prato umido oligotrofico (*Molinion coeruleae*); 3) vegetazione erbacea perenne e disorganizzata al margine superiore della stazione.

Elenco delle specie raccolte

Con l'unica eccezione costituita da un sommario rilievo condotto in prossimità della vetta del M.Barro, tutto il materiale è stato raccolto dal Dr. Davide Sassi nel corso di ricerche che si sono svolte per buona parte al difuori delle stazioni di raccolta (staz. 1-9) scelte come base per uno studio dei biotopi prativi; per ogni specie, comunque, viene qui fornita un'indicazione sufficientemente precisa delle singole località di rinvenimento.

Grammoptera ruficornis (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: numerose latifoglie arboree e arbustive.
5 esemplari raccolti fra il 9.III e il 30.V nelle staz. 3, 6 e 8, in un prato della Val Faè vicino alla staz. 7 e, sul versante meridionale, ai margini di un sentiero che dall'eremo va alla Sella della Pila.

Pseudallosterna (Pseudovadonia) livida (Fabricius)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: numerose latifoglie (in realtà la larva si nutre dei miceli di funghi saprofiti su radici morte).
2 esemplari raccolti nella staz. 7 (17.VII.1992, lg. Sassi).
Osservazioni: la specie sembrerebbe rappresentata, in gran parte d'Italia, dalla ssp. *pecta* Daniel, il cui esatto status sistematico, peraltro, necessita di revisione.

Leptura (Rutpela) maculata Poda
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie, più raramente conifere.
6 esemplari raccolti nelle staz. 4, 5, e 8 (15.VII.1991/2, lg. Sassi).

Stenurella bifasciata (Müller)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose conifere e latifoglie.
3 esemplari raccolti tra l'8.VII e il 2.VIII nelle staz. 2, 3 e 4.

Stenopterus rufus (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
3 esemplari raccolti in luglio nelle staz. 4, 7 e 8 e presso la vetta.

Deilus fugax (Olivier)
Corotipo: Mediterraneo (MED).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: svariate Fabaceae della tribù Genisteae.
Un unico reperto (presso la vetta, 6.VII.1990, lg. Sassi).

Cerambyx scopolii (Füssly)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
3 esemplari raccolti nei boschi sul versante occidentale della vetta del M. Barro, 8.V.1992, lg. Sabbadini & Pesarini).

Phymatodes testaceus (Linneo)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
Un unico reperto sul versante meridionale, ai margini di un sentiero che dall'eremo conduce alla Sella d. Pila (30.V.1990, lg. Sassi).

Poecilium (s.str.) alni (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: numerose latifoglie.
Un unico reperto (staz. 2, 23.V.1991, lg. Sassi).

Xylotrechus arvicola (Olivier)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
Un unico reperto sul versante meridionale, ai margini di un sentiero che dall'eremo conduce alla Sella d. Pila (6.VII.1990, lg. Sassi).

Clytus arietis (Linneo)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia.
Piante ospiti: numerose latifoglie.
Un esemplare raccolto nella staz. 2 (24.VI.1989) ed uno ai margini di un sentiero che dall'eremo conduce alla Sella d. Pila (30.V.1990, lg. Sassi).

Clytus rhamni Germar ssp.***bellieri*** Gautier
Corotipo: W-Europeo (WEU).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
Due esemplari raccolti nella staz. 2 (12.VI.1989 e 25.VI.1992, lg. Sassi) ed uno nella staz. 4 (15.VII.1991, lg. Sassi).

Chlorophorus pilosus (Forster) ssp.***glabromaculatus*** (Goeze)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
Un unico reperto nel bosco al margine della strada asfaltata che sale verso il Monumento dell'Alpino (6.VII.1990, lg. Sassi).

Chlorophorus varius (Müller)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose latifoglie.
Alcuni esmplari raccolti in luglio e agosto nelle staz. 2 e 9.

Chlorophorus sartor (Müller)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.

Piante ospiti: numerose latifoglie.
Alcuni esemplari raccolti da fine giugno a inizio agosto nelle staz. 2, 3, 4, 5 e 8, e presso la vetta.
Osservazioni: nell'ambito di questa specie, è possibile distinguere una forma orientale ed una occidentale (cui appartengono le popolazioni italiane) discretamente distinte, verosimilmente a livello sottospecifico. Poiché però, come rilevato anche da Sama (1988, p.125) non è per il momento possibile assegnare alla specie una patria classica, non indicata nella descrizione originale, la situazione nomenclatoriale delle eventuali sottospecie non può essere attualmente precisata. Sembra comunque verosimile che alla sottospecie italiana, ove questa non andasse identificata con la forma nominale, debba essere attribuito il nome di *massiliensis* (Linneo) e non quello di *infensus* Plavilstshikov, come spesso indicato in letteratura, che ha per patria classica il Caucaso.

Parmena unifasciata (Rossi)
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutta Italia.
Piante ospiti: numerose latifoglie, più di rado conifere.
Un unico reperto (staz. 3, 20.IX.1989, lg. Sassi).

Lamia textor (Linneo)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Italia settentrionale e centrale, Basilicata, Sicilia.
Piante ospiti: specie dei generi *Salix, Populus, Betula, Alnus* e *Morus*.
Un unico reperto (staz. 6, 24.IV.1992, lg. Sassi).

Agapanthia (s.str.) cardui (Linneo)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose piante erbacee di svariate famiglie.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2, 6 e 8.

Anaesthetis testacea (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Campania, Calabria, Sicilia.
Piante ospiti: numerose latifoglie, ma soprattutto querce *(Quercus)*.
Alcuni esemplari raccolti da maggio a luglio nelle staz. 2 e 6, in un prato sotto il Monumento all'Alpino e ai margini di un sentiero che dall'eremo va alla Sella d. Pila.

Exocentrus lusitanus (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Trentino-Alto Adige, Friuli-Venezia Giulia. La specie risulta nuova per la Lombardia.
Piante ospiti: *Tilia cordata*.
Un unico reperto ai margini di un sentiero che dall'eremo va alla Sella della Pila (30.V.1990, lg. Sassi).

Exocentrus adspersus Mulsant
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Puglia, Sicilia.
Piante ospiti: svariate specie di *Fagales*.
Un esemplare raccolto nella staz. 1 (12.VII.1991, lg. Sassi), ed uno nella staz. 4 (10.VI.1990).

Pogonochoerus hispidus (Linneo)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: numerose latifoglie.
Un unico reperto (staz. 3, 14.III.1990, lg. Sassi).

Saperda (Compsidia) populnea (Linneo)
Corotipo: Olartica (OLA).
Presenza in Italia: Italia settentrionale e centrale, Basilicata, Calabria, Sicilia.
Piante ospiti: pioppi (*Populus*) o, più di rado, salici (*Salix*).
Un unico reperto (staz. 2, 27.V.1989, lg. Sassi).

Phytoecia (s.str.) cylindrica (Linneo)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale e centrale, Campania, Puglia, Basilicata.
Piante ospiti: diverse specie di *Apiaceae*.
Un esemplare raccolto nella staz. 8 (16.V.1990, lg. Sassi) e due nei boschi della Val Faè (23.V.1991, lg. Sassi).

Phytoecia (s.str.) pustulata (Schrank)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: tutta Italia.
Piante ospiti: alcune specie di *Asteraceae*, ma soprattutto *Achillea millefolium*.
Alcuni esemplari raccolti in maggio nelle staz. 1, 8 e 9.

Phytoecia (s.str.) virgula (Charpentier)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: svariate specie di *Asteraceae*.
Alcuni esemplari raccolti in maggio nella staz. 2 e in luglio nel bosco che costeggia la strada asfaltata che sale verso il Monumento all'Alpino.

Oberea (s.str.) linearis (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Calabria, Sicilia.
Piante ospiti: svariate latifoglie, ma soprattutto *Corylus avellana*.
Un unico reperto (staz. 6, 19.V.1992).

Tabella 1 - Tabella riassuntiva delle specie raccolte.

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Grammoptera ruficornis			+			+		+		+
Pseudallosterna livida							+			
Leptura maculata				+	+			+		
Stenurella bifasciata		+	+	+						
Stenopterus rufus				+			+	+		+
Deilus fugax										+
Cerambyx scopolii										+
Phymatodes testaceus										+
Poecilium alni		+								
Xylotrechus arvicola										+
Clytus arietis		+								+
Clytus rhamni bellieri		+		+						

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Chlorophorus pilosus glabromaculatus										+
Chlorophorus varius		+							+	
Chlorophorus sartor		+		+	+			+		+
Parmena unifasciata			+							
Lamia textor						+				
Agapanthia cardui	+	+				+		+		
Anaesthetis testacea		+				+				+
Exocentrus lusitanus										+
Exocentrus adspersus	+			+						
Pogonochoerus hispidus			+							
Saperda populnea		+								
Phytoecia cylindrica								+		+
Phytoecia pustulata	+							+	+	
Phytoecia virgula							+			+
Oberea linearis						+				

Tabella 2 - Spettro corologico delle specie raccolte. Le sigle dei corotipi fondamentali sono ricavate dal lavoro di Vigna Taglianti et al. (1991).

Corotipo	n° specie	% sul totale
Europeo (EUR)	8	29,63
Sibirico-Europeo (SIE)	5	18,52
Europeo-Mediterraneo (EUM)	3	11,11
Centroasiatico-Europeo (CAE)	3	11,11
W-Paleartico (WPA)	2	7,41
Olartico (OLA)	1	3,70
Asiatico-Europeo (ASE)	1	3,70
Mediterraneo (MED)	1	3,70
Centroeuropeo (CEU)	1	3,70
S-Europeo (SEU)	1	3,70
W-Europeo (WEU)	1	3,70
TOTALE	27	100,00

Ripartizione delle specie in base alle categorie corologiche

Lo spettro corologico delle specie raccolte (tabella 2) mostra una dominanza di elementi ad ampia distribuzione e una scarsissima presenza di elementi mediterranei; lo stesso dato emerge, con maggior evidenza, dalla fig.1, dove i corotipi sono stati raggruppati per categorie sintetiche.
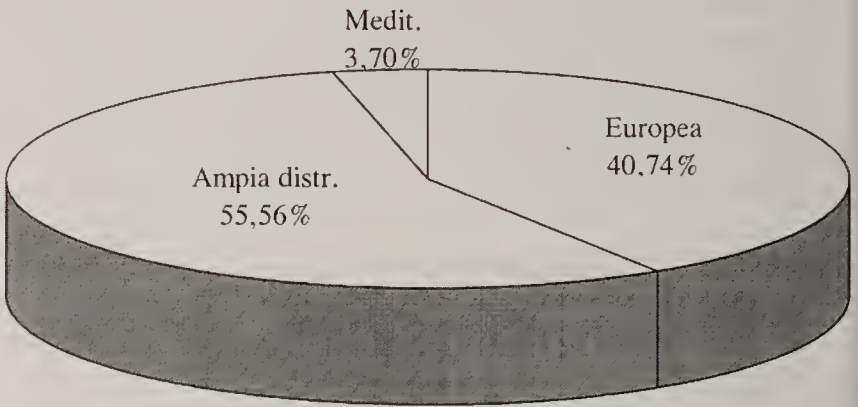
Fig. 1 - Corotipi raggruppati per categorie sintetiche.

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I Crisomelidi (Coleoptera Chrysomelidae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Vengono presentati i risultati di una pluriennale indagine faunistica sul rilievo brianteo del Monte Barro. Oltre ad un elenco delle 152 specie di Crisomelidi censite (otto delle quali risultano nuove per la fauna lombarda) sono fornite note biologiche per numerosi taxa e considerazioni sistematiche su alcune specie di particolare interesse: è studiata la variabilità della lunghezza (Lp) e della larghezza (lp) del pronoto in un piccolo campione di *Lilioceris merdigera* del Monte Barro posto a confronto con un campione di *Lilioceris schneideri* raccolto in Abruzzo; sono descritte le differenze morfologiche e morfometriche fra *Longitarsus minusculus* e *Longitarsus anacardius*; è illustrata la variabilità dell'edeago e della silhouette elitrale in *Longitarsus pinguis*, per il quale si evidenzia l'esistenza di una forma appenninica leggermente diversa da quella alpina; è studiata la variabilità di Le, Lp, Lt, Ld in campioni del Monte Barro di *Psylliodes toelgi* e *Ps. brisouti*. Sono raffigurati in visione ventrale e laterale gli edeagi di esemplari del Monte Barro di *Longitarsus minusculus*, *Longitarsus pinguis*, *Altica carinthiaca*, *Asiorestia crassicornis*, *Dibolia foersteri*, *Psylliodes brisouti e Psylliodes toelgi*. Sono riportati dati biologici di *Cassida subreticulata* e ne vengono descritte e raffigurate la larva al quinto stadio e la pupa. Le raccolte sono state effettuate prevalentemente in 8 stazioni prative situate all'interno del parco regionale e selezionate in base a criteri fitosociologico-vegetazionali: la maggior parte di queste stazioni (1, 3, 4, 7 e 8) sono prati regolarmente falciati e la stazione 5 si distingue dalle rimanenti per la presenza di elementi di brughiera. Abbiamo confrontato queste stazioni costruendo curve di k-dominanza, calcolando indici di diversità (i valori più bassi dell'indice di Shannon si sono ottenuti nelle stazioni 3,7,8) ed effettuando infine un'analisi numerica con gli indici di Sörensen e di Sokal-Michener per mettere in evidenza il grado di affinità fra le stazioni indagate. Le raccolte sono state effettuate anche ai margini del fragmiteto che costeggia il lago di Annone, in località Sala al Barro (staz. 9). Dal punto di vista zoogeografico prevalgono nei Crisomelidi le specie ampiamente distribuite nella regione paleartica; i corotipi mediterranei costituiscono una percentuale molto piccola (1.3%) delle specie raccolte, ma vi è un'importante presenza (18%) di elementi sudeuropei, in accordo con le caratteristiche insubriche dell'area indagata. Conclude il lavoro un quadro sinottico della fenologia delle specie.

Abstract - Leaf beetles (Coleoptera Chrysomelidae) from Monte Barro (Italy, Lombardy, Lecco).
This paper is the result of a faunistical research on the Chrysomelid-beetles of Monte Barro Regional Park, which is placed at the southeast end of Como Lake, in face of the massif of the Grigne. The authors give the list of 152 species collected during four years of entomological survey, with information on host plants, distributional pattern and distribution in Italy for each taxon and biological notes for many of them. Noteworthy distributional data are reported: *Longitarsus exoletus*, *L. foudrasi*, *L. brunneus*, *L. minusculus*, *Altica carinthiaca*, *Asiorestia crassicornis*, *Dibolia foersteri* and *Psylliodes brisouti* are new to Lombardia; *Cryptocephalus bimaculatus* is new to Calabria; *Cr. flavipes* in nex to Sardegna *Aphthona atrovirens* is new to Molise; *Longitarsus pinguis* is new to Liguria, Molise and Campania; *Asiorestia crassicornis* is new to Emilia-Romagna; *Psylliodes toelgi* is new to Lazio. Systematical comments on a few species are appended, i. e.: information is given on the variability of pronotal length (Lp) and width (lp) in a little sample of *Lilioceris merdigera* from Monte Barro, which is compared with a sample of *Lilioceris schneideri* from Abruzzo; morphologic and morphometric differences between *Longitarsus minusculus* and *Longitarsus anacardius* are described; in consequence of a study on the variability of aedeagus and elytral silhouette in *L. pinguis*, the existence of an Apenninic form somewhat different from the Alpine one is emphasized; information is given on the variability of elytral length (Le), pronotal length (Lp), length of hind tibia (Lt) and length of prolongation of hind tibia beyond tarsal insertion (Ld) in samples of *Psylliodes brisouti* and *Ps. toelgi* from Monte Barro. Nymph and fifth larval instar of *Cassida subreticulata* are described. Aedeagi of specimens from Monte Barro belonging to following species are figured in ventral and lateral view: *Longitarsus minusculus*, *L. pinguis*, *Altica carinthiaca*, *Asiorestia crassicornis*, *Dibolia foersteri*, *Psylliodes brisouti* and *Psylliodes toelgi*. Most specimens have been collected in 8 sampling-sites placed inside the Park and selected on the ground of physionomic-vegetational criteria. Most of these sampling-sites (1, 3, 4, 7 and 8) are regularly mowed and peculiar to sampling-site 5 is the presence of heath elements. We have compared these sampling-sites by means of k-dominance curves, indexes of diversity (sites 3, 7 and 8 give comparatively small values of Shannon's index) and cluster analysis, in order to point out their degree of affinity. Also a grassland on the border of the swamp running along the side of Annone Lake, in the district of Sala al Barro, has been investigated (site 9). From the zoogeographic point of view species widely distributed in the Palaearctic region are prevailing, there is a very low percentage (1.3 %) of Mediterranean elements, but a comparatively high percentage (18 %) of south-European taxa, in agreement with the Insubric character of the investigated area. A synoptic phenologic table is given in the end of the work.

Key words: Monte Barro, Chrysomelidae, Phenology, Geographic distribution.

Il Monte Barro è un modesto rilievo situato all'estremo limite sudorientale del Triangolo Lariano, in posizione dominante la città di Lecco e prospicente al massiccio delle Grigne. Per il suo rilevante interesse ambientale è attualmente un parco naturale della Regione Lombardia.

Questo studio, che presenta il risultato di quattro anni di raccolte di coleotteri crisomelidi nell'area in oggetto, è stato condotto secondo due direttrici. In primo luogo si è cercato di censire tutte le specie presenti nell'intera area studiata, utilizzando le consuete tecniche di raccolta (a vista, retino da sfalcio, ombrel-

lo entomologico). Inoltre, allo scopo di mettere in luce eventuali caratterizzazioni faunistiche nell'ambito delle zone prative del Parco, è stato condotto un confronto statistico del popolamento crisomelidologico tra otto diverse stazioni, selezionate sulla base della fisionomia della vegetazione. A causa della limitata estensione del territorio indagato la caratterizzazione delle stazioni è piuttosto modesta, l'analisi ha permesso comunque di evidenziare alcuni aspetti significativi. Ad eccezione della stazione 5, che si differenzia in modo evidente per la presenza dell'elemento acidofilo di brughiera, le altre stazioni possono essere inquadrate in una tipologia di tensione tra gli ordini non climacici *Arrhenatheretalia elatioris* Pawl. 1828 e *Brometalia erecti* Br.-Bl. 1936. Il primo ordine rappresenta le comunità di prato regolarmente falciato, di condizioni meso-eutrofiche, suolo profondo, generalmente favorite dalla presenza di falda superficiale, e si esprime attraverso gli elementi dell'associazione *Arrhenatheretum elatioris* Br.-Bl. ex Scherr. 1925 (*Arrhenatherum elatius, Trisetaria flavescens, Dactylis glomerata, Silene vulgaris, Ranunculus acris, Rhinanthus alectorolophus, Plantago lanceolata* ecc.). Il secondo ordine, legato al dinamismo naturale extraforestale, rappresenta le comunità di prateria semiarida che ricoprono suoli molto scarni o substrati litoidi, spesso in forte pendenza, all'inizio di una serie dinamica che porta alla ricostruzione della copertura forestale. La combinazione specifica ricorrente (*Bromopsis erecta, Dianthus carthusianorum, Lilium bulbiferum, Trinia glauca, Helianthemum nummularium* ssp. *obscurum, Sanguisorba minor* ssp. *muricata, Potentilla neumanniana* ecc.) consente di attribuire tali espressioni all'alleanza *Mesobromion erecti* (Br.-Bl. & Moor 1938) Knapp 1942. Il dinamismo naturale, come accennato, porta in tempi brevi alla ripresa della copertura forestale, che per tutte le stazioni si identifica con il climax di un querceto a rovere (*Quercus petraea*), roverella (*Q. pubescens*), orniello (*Fraxinus ornus*) e carpinello (*Ostrya carpinifolia*), inquadrabile nell'alleanza *Quercion pubescenti-petreae* Br.-Bl. 1932, attualmente vicariata dalle formazioni boschive dell'*Orno-Ostryon*. Al momento delle raccolte, tutte le stazioni non più gestite presentavano un'evidente ripresa dinamica, come si è potuto constatare dalla costante presenza di significativi elementi dell'alleanza *Geranion sanguinei* Tx. 1961, tra cui *Geranium sanguineum, Origanum vulgare, Vincetoxicum hirundinaria, Knautia drymeia* ssp. *centrifrons, Teucrium chamaedrys, Thymus pulegioides* ecc.

Le raccolte hanno interessato anche una piccola superficie in località Sala al Barro, situata a ridosso del *Phragmitetum* che costeggia il Lago di Annone e denominata nel testo Stazione 9. Questa stazione non verrà confrontata direttamente con le altre in quanto si differenzia in modo evidente.

Fig. 1 - Carta del Monte Barro con l'ubicazione delle stazioni 1-9.

Caratteri stazionali specifici

Per le prime otto stazioni vengono indicate le specie esclusive (specificità), e le tre specie più comuni con il relativo indice di dominanza (sensu Berger & Parker, 1970). Si tratta di un indice molto semplice (numero di esemplari di ogni specie sul numero totale di esemplari raccolti), che però fornisce un'accettabile stima della diversità di un popolamento, tenendo anche conto della buona correlazione che mostra nei confronti del più popolare indice di Simpson. Viene inoltre riportato l'indice di dominanza di Margalef $Dmg = (S-1)/ln(N)$ dove S è il numero di specie censite e N il numero totale degli individui raccolti. Per la stazione nove, non direttamente comparabile con le precedenti, non vengono indicate le specificità.

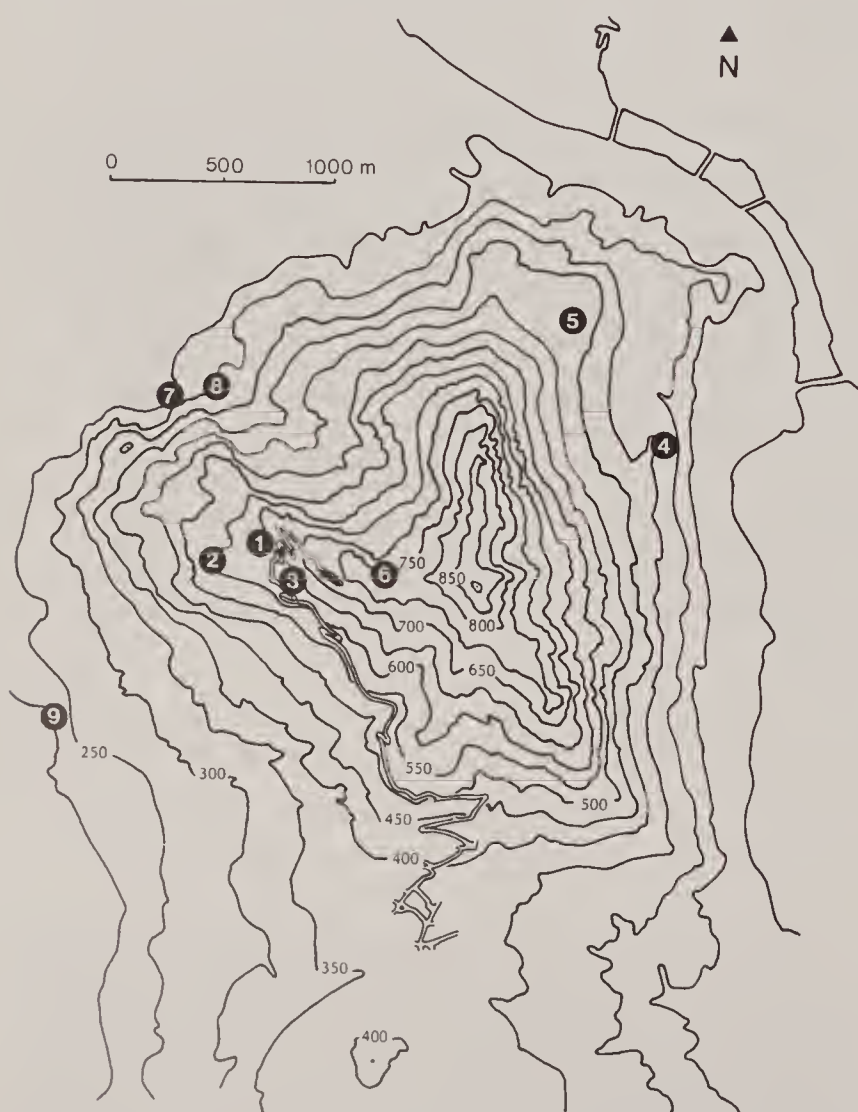
Stazione 1 (Fig. 67): Località Piani di Barra, 610 m, esp. W, dal 1990 interessata da scavi archeologici in rapporto al cosiddetto *Grande Edificio.* Consistente presenza di prato falciabile che indica una attività di foraggio residua, testimoniata anche dalla non significatività del mantello.

Specificità: *Smaragdina aurita, Longitarsus holsaticus.* Dominanze: *Longitarsus luridus (0,245), Podagrica fuscicornis (0,179), Sphaeroderma rubidum (0,084).* 40 specie censite; 559 esemplari. Dmg = 6,16.

Stazione 2 (Fig. 67): Località Piani di Barra, 600 m, esp. W, dal 1990 interessata da scavi archeologici in rapporto al cosiddetto *Edificio II.* Leggera prevalenza di prateria e mantello su prato falciabile, cioè netta risposta all'abbandono di una gestione a foraggio già indebolita.

Specificità: *Cryptocephalus trimaculatus, Labidostomis tridentata, Leptinotarsa decemlineata, Lilioceris lilii, Mantura obtusata, Psylliodes brisouti, Psylliodes instabilis, Crepidodera aurea.* Dominanze: *Aphthona venustula (0,122), Cryptocephalus flavipes (0,111), Longitarsus succineus (0,092).* 65 specie censite; 931 esemplari. Dmg = 9,37.

Stazione 3: Conca prativa a monte del *Monumento all'Alpino*, 630 m, esp. W. Convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Specificità: *Longitarsus tabidus, Phyllotreta aerea, Phyllotreta ochripes, Timarcha nicaeensis, Chaetocne-*

ma concinna, Chrysolina polita, Chrysolina rossia. Dominanze: *Longitarsus luridus (0,423), Longitarsus succineus (0,111), Longitarsus pratensis (0,082).* 56 specie censite; 2182 esemplari. Dmg = 7,15.

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion erecti* (*Thalictrum minus, Arabis collina*) è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.

Specificità: *Chrysolina fastuosa, Chrysolina orical-*

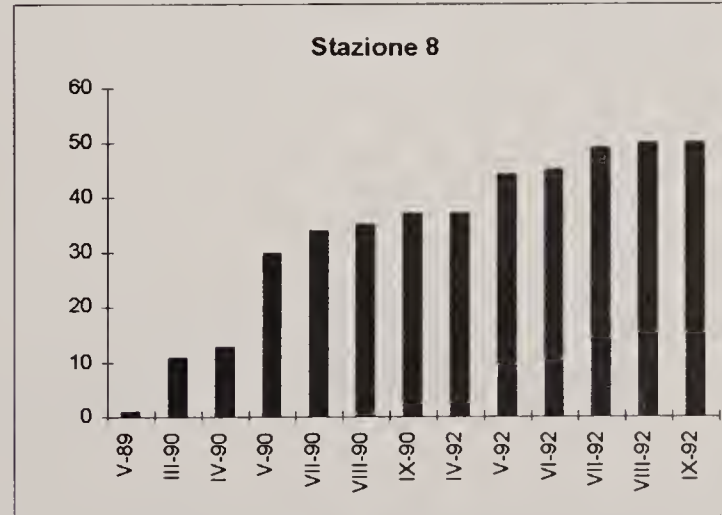
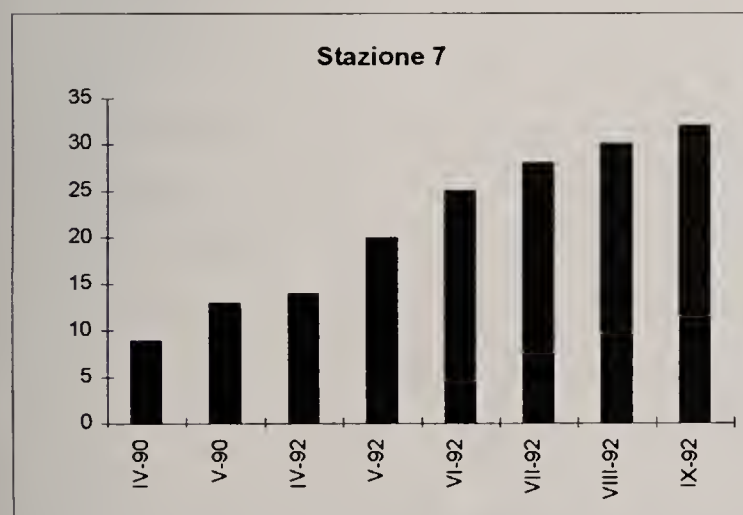
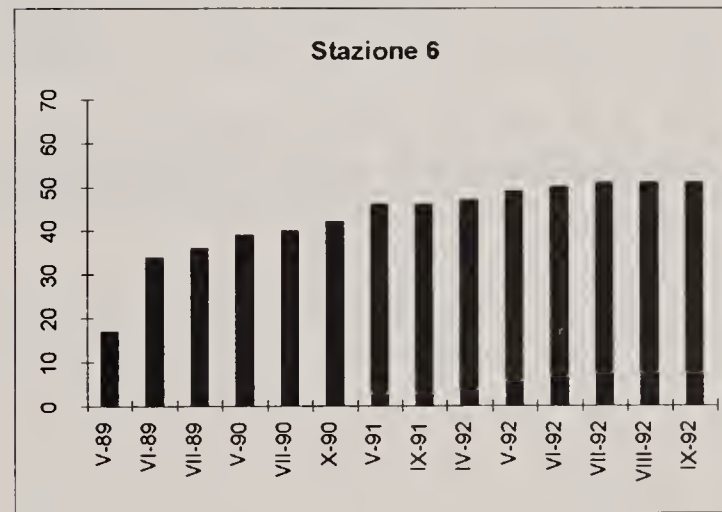
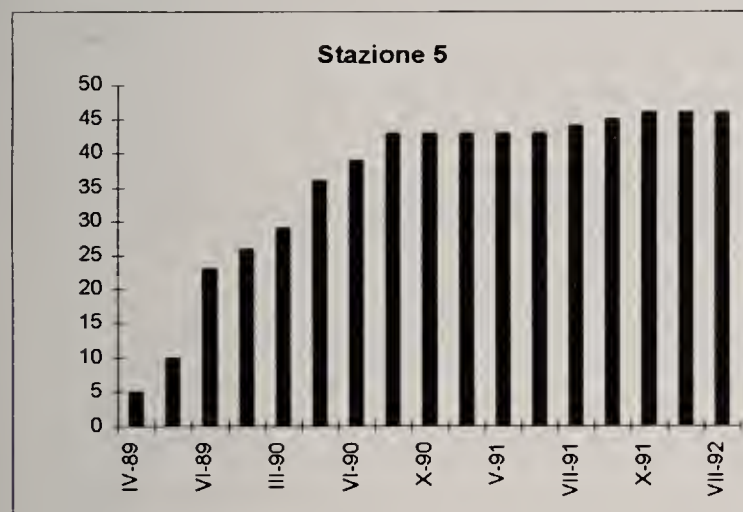
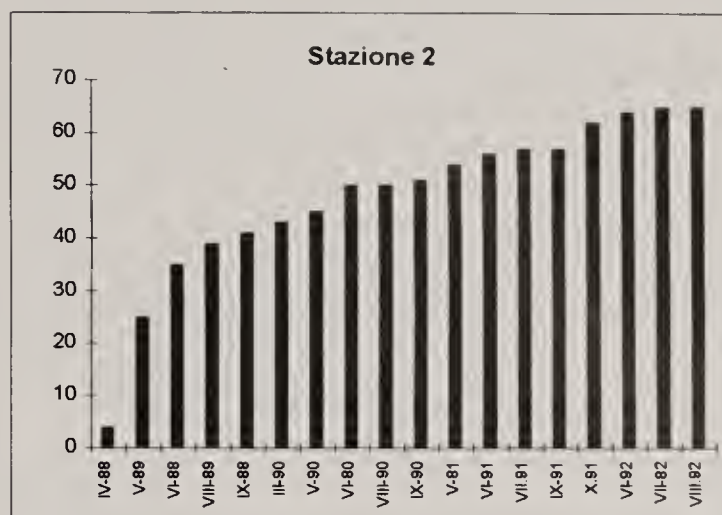



Fig. 2 - Diagrammi di saturazione delle specie censite nei periodi di raccolta.

cia, Clytra appendicina, Aphthona pygmaea, Argopus ahrensi, Cassida subreticulata, Psylliodes cupreus, Smaragdina flavicollis, Phyllotreta nemorum. Dominanze: *Longitarsus luridus (0,182), Longitarsus exoletus (0,079), Longitarsus pratensis (0,069).* 61 specie censite; 1341 esemplari. Dmg = 8,33.

Stazione 5 (Fig. 67): Località Pian Sciresa, 435 m, esp. NE. Prato arido con montarozzi residuali a brughiera. Si caratterizza meglio di tutte le altre stazioni per la presenza dell'elemento di brughiera, accompagnato da *Cytisus emeriflorus*, endemismo calcicolo SE-alpico. Per il resto il livello di base è costituito da prateria a *Brachypodium rupestre* ssp. *caespitosum.*

Specificità: *Dibolia foersteri, Crepidodera aurata, Crytocephalus fulvus, Cryptocephalus primarius.* Dominanze: *Aphthona herbigrada (0,116), Cryptocephalus labiatus (0,097), Cryptocephalus transiens (0,085).* 46 specie censite; 941 esemplari. Dmg = 6,57.

Stazione 6 (Fig. 67): Superfici prative lungo il sentiero della «Cresta occidentale», che dall'edificio dell'ex sanatorio sale alla vetta, 750 m, esp. S. Prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura. Forte influsso dell'elemento prenemorale, con tendenza a un *Quercetum pubescentis* s. l. L'elemento di mantello ha scarso peso.

Specificità: *Galeruca pomonae, Longitarsus obliteratus.* Dominanze: *Aphthona herbigrada (0,336), Longitarsus helvolus (0,136), Longitarsus obliteratus (0,086).* 51 specie censite; 1678 esemplari. Dmg = 6,73.

Stazione 7 (Fig. 67): Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. Superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8, ma più aperta e con qualche elemento in più di *Mesobromion.*

Specificità: nessuna. Dominanze: *Longitarsus pratensis (0,251), Longitarsus luridus (0,214), Longitarsus succineus (0,117).* 32 specie censite; 426 esemplari . Dmg = 5,12.

Stazione 8 (Fig. 67): Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. Superficie prativa terrazzata, irregolarmente gestita e contornata da un bosco con notevoli contrassegni mesofili. Ciò è conseguenza dell'esposizione fresca e di un maggiore sviluppo di suolo. Sono comunque sempre presenti gli elementi di prateria.

Specificità: *Labidostomis longimana, Cryptocephalus loreyi, Oomorphus concolor, Longitarsus minusculus, Sphaeroderma testaceum.* Dominanze: *Longitarsus luridus (0,274), Longitarsus pratensis (0,224), Longitarsus salviae (0,169).* 50 specie censite; 1046 esemplari. Dmg = 5,05.

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Vi si evidenziano tre aspetti essenziali: 1) il canneto (*Phragmitetum australis*) con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto (*Caricetum elatae*) e residui di boscaglia ripariale (*Salicion cinereae*). 2) il prato umido oligotrofico (*Molinion coeruleae*); 3) vegetazione erbacea perenne e disorganizzata, al margine superiore della stazione, riconducibile alle classi *Artemisietea vulgaris* e *Plantaginetea majoris.*

Dominanze: *Aphthona coerulea (0,218), Lythraria salicariae (0,083), Asiorestia transversa (0,072).* 59 specie censite; 1681 esemplari. Dmg = 7,43.

Confronto statistico delle stazioni

Le campagne di ricerca nel Parco hanno fruttato la raccolta di 12.422 esemplari appartenenti a 152 specie, alcune di particolare interesse o inedite per la Lombardia.

Allo scopo di valutare l'accuratezza con cui i censimenti sono stati condotti, abbiamo costruito per le stazioni 1-8 i diagrammi di saturazione (Fig. 2), che indicano il progressivo incremento di specie nei successivi periodi di raccolta. L'altezza degli istogrammi tende ad un limite (altezza di saturazione) che corrisponde al numero ideale di specie che con le tecniche in uso è possibile censire ed è quindi indipendente dal numero delle raccolte ulteriori. L'andamento dei diagrammi sembra mostrare che per tutte le stazioni, tranne 1, 7 e forse 8, si raggiungono valori molto pros-

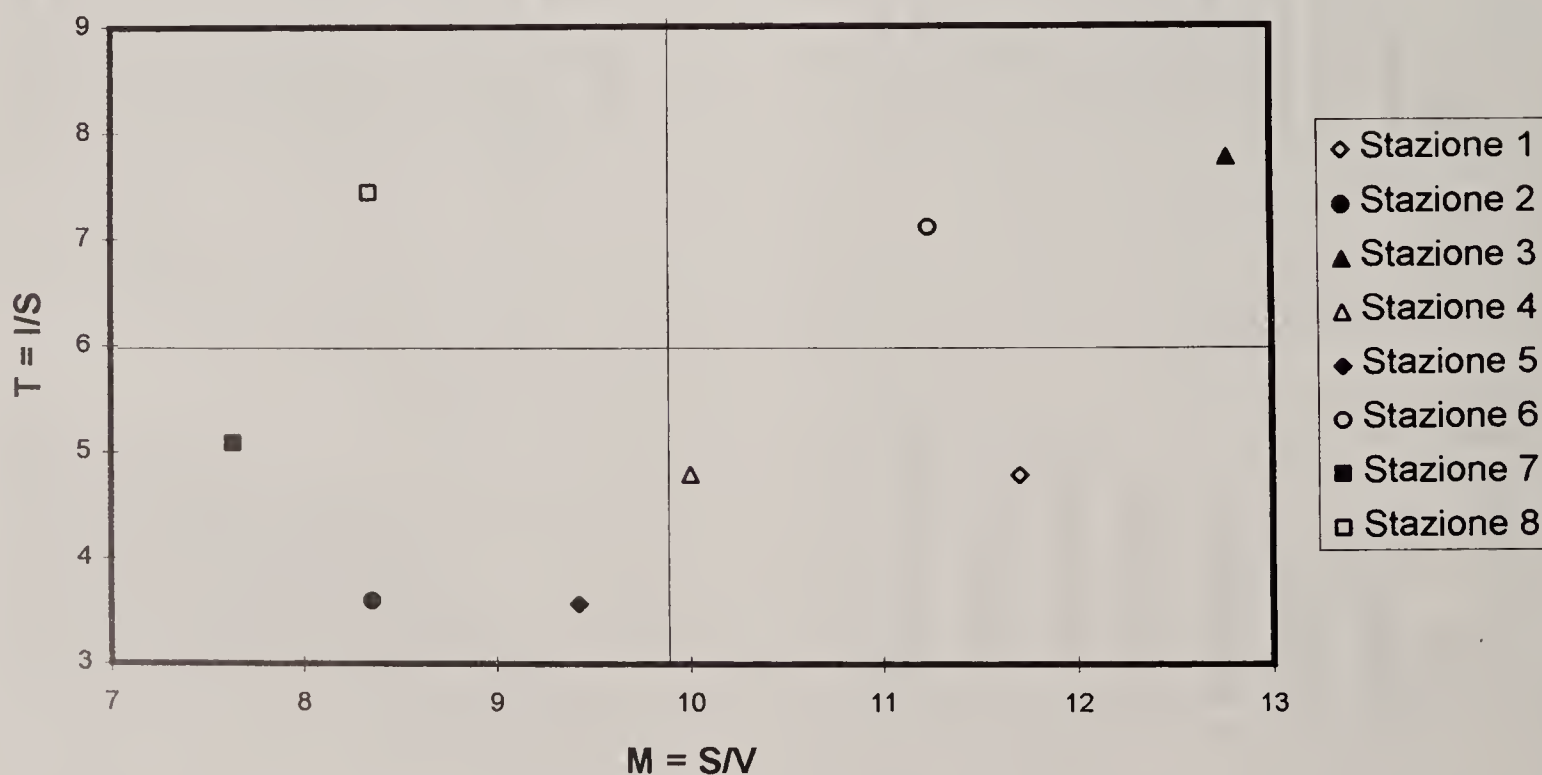



Fig. 3 - Confronto fra numero medio di individui raccolti per ciascuna specie (T) e numero medio di specie censite per ogni raccolta effettuata. Per la spiegazione vedi testo.

simi all'altezza di saturazione. Riteniamo pertanto che il quadro ottenuto dalle nostre indagini sia sufficientemente rappresentativo.

Malgrado la complessità dell'ambiente studiato abbia impedito di effettuare raccolte quantitative, è sembrato comunque utile ricorrere ad alcuni indici ecologici per un confronto delle stazioni. In primo luogo abbiamo valutato le differenze nella struttura del popolamento delle stazioni 1-8 confrontando il numero medio di individui raccolti per ciascuna specie (T=I/S) e il numero medio di specie censite per ogni raccolta effettuata (M=S/V), dove I è il numero di individui complessivamente raccolti nella stazione in tutte le uscite, S è la sommatoria di tutte le specie raccolte nella stazione nel totale delle uscite, V è il totale delle uscite effettuate nella stazione (Pesarini, 1986). Il calcolo di tali rapporti permette di rendere indipendenti i dati dal numero delle uscite. I valori ottenuti sono riportati nella tabella 1 e graficamente nella figura n. 3.

Tabella 1 - Valori di T e di M (v. testo) relativi alle stazioni 1-8.

	Staz. 1	Staz. 2	Staz. 3	Staz. 4	Staz. 5	Staz. 6	Staz. 7	Staz. 8
T	4,778	3,595	7,765	4,789	3,564	7,110	5,071	7,447
M	11,700	8,355	12,773	10,000	9,429	11,238	7,636	8,294

Nel diagramma emergono alcuni raggruppamenti quali 3; 6, caratterizzato da un elevato numero medio di specie e di esemplari per specie, e 2; 5; 7 con caratteristiche opposte. La stazione 8 presenta un alto numero di esemplari per specie ma una bassa varietà delle medesime, mentre il complesso 1; 4 manifesta una tendenza contraria.

In secondo luogo abbiamo stimato la diversità e l'*evenness* all'interno delle stazioni 1-8 utilizzando i relativi indici di Shannon. Per valutare i confronti possibili, abbiamo determinato le curve di k-dominanza (Fig. 4), calcolando l'abbondanza relativa proporzionale delle k specie presenti in una stazione, ed esprimendo graficamente i risultati in forma di percentuale cumulativa. Lambshead et al. (1983) hanno infatti osservato che, se le curve di k-dominanza si intersecano intorno a metà del loro tragitto, il confronto degli indici di diversità non può considerarsi attendibile. Nella tabella 2 sono riportati i valori (log base 2) degli indici di diversità (in tondo) e di *evenness* (in corsivo), evidenziando i confronti possibili (+).

Tabella 2 - Valori (log base 2) degli indici di diversità (in tondo) e di *evenness* (in corsivo) relativi alle stazioni 1-8. I confronti possibili sono indicati con +.

	Staz. 1 3,89 *0,73*	*Staz. 2* 4,73 *0,79*	*Staz. 3* 3,38 *0,58*	*Staz. 4* 4,57 *0,77*	*Staz. 5* 4,61 *0,83*	*Staz. 6* 3,75 *0,66*	*Staz. 7* 3,56 *0,71*
Staz. 8 3,48 *0,62*	+	+	–	+	+	+	–
Staz. 7 3,56 *0,71*	+	+	–	+	+	+	
Staz. 6 3,75 *0,66*	–	+	+	+	+		
Staz. 5 4,61 *0,83*	+	–	+	–			
Staz. 4 4,57 *0,77*	+	–	+				
Staz. 3 3,38 *0,58*	+	+					
Staz. 2 4,73 *0,79*	+						

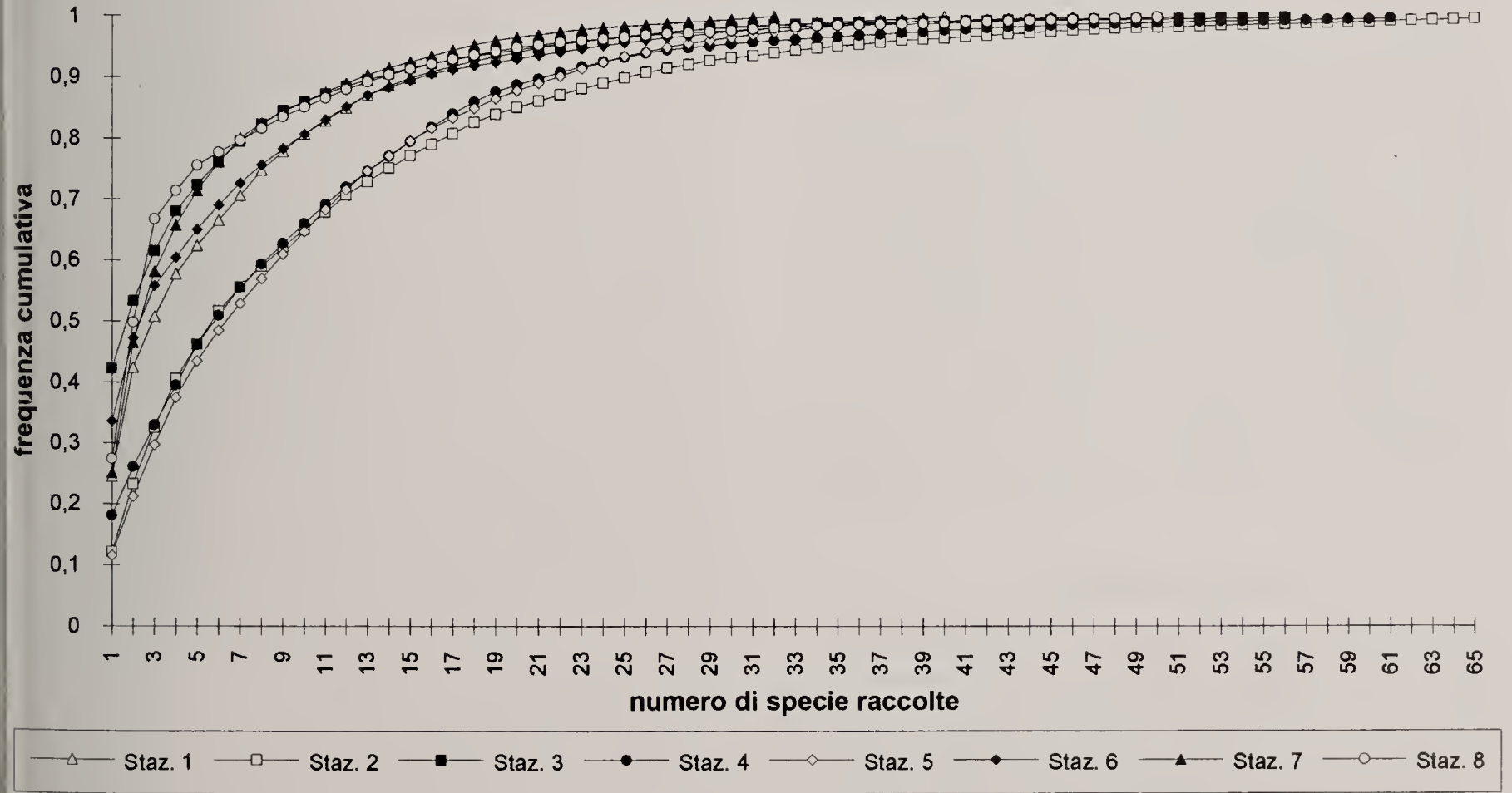



Fig. 4 - Curve di k-dominanza relative alle stazioni 1-8 su tutti gli anni delle raccolte.

Fig. 5.1 - Curve di k-dominanza relative al complesso delle stazioni 1-8 nei diversi mesi di campionamento del 1990

Fig. 5.2 - Curve di k-dominanza relative alla stazione 9 nei diversi mesi di campionamento del 1990.

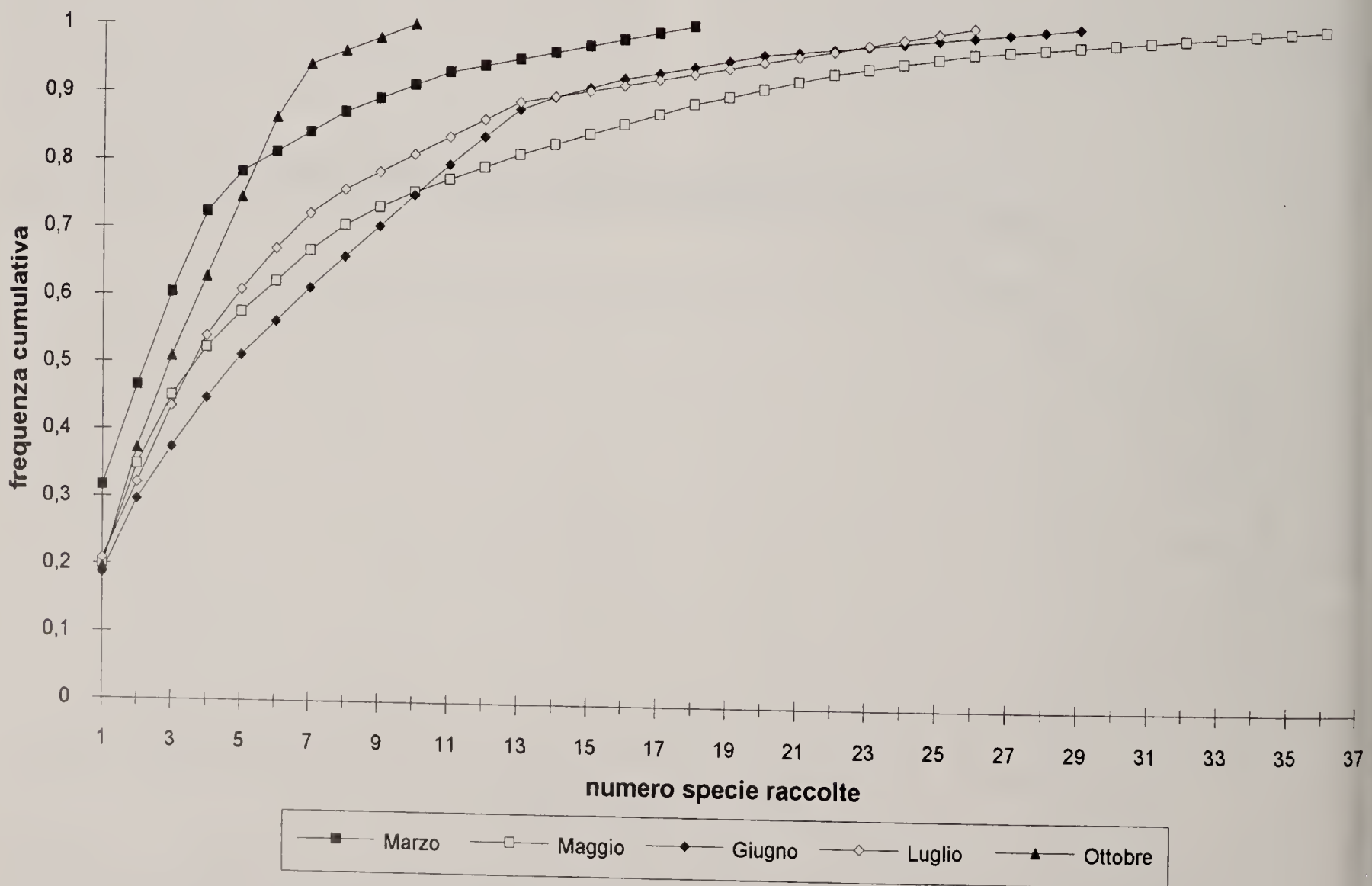
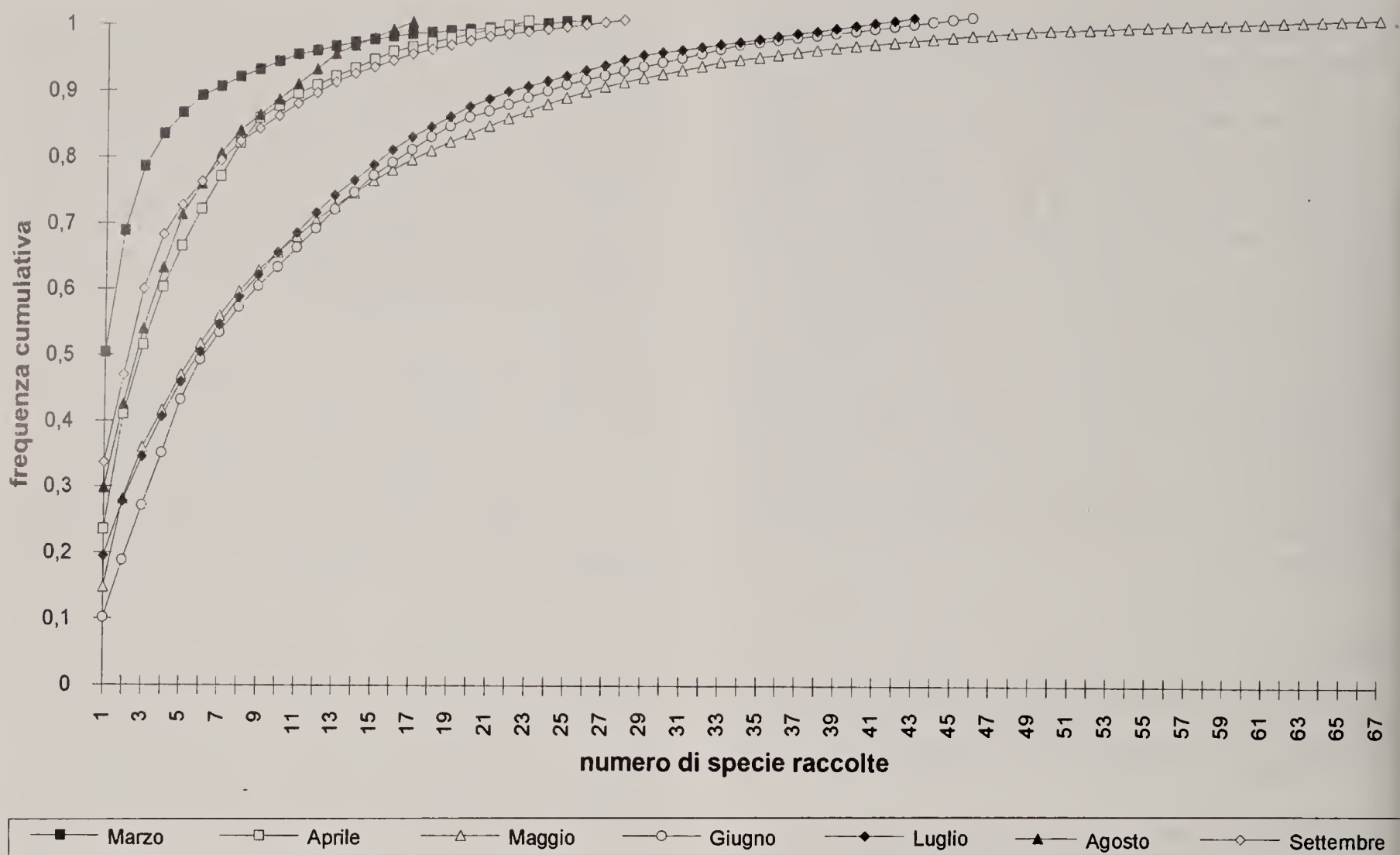



Tabella 3 - Valori (log base 2) degli indici di diversità (in tondo) e di *evenness* (in corsivo) relativi ai mesi di raccolta del 1990 nelle stazioni 1-8.

	Marzo 2,55 *0,54*	*Aprile* 3,59 *0,79*	*Maggio* 4,73 *0,78*	*Giugno* 4,72 *0,85*	*Luglio* 4,54 *0,84*	*Agosto* 3,36 *0,82*
Settembre 3,43 *0,71*	+	–	+	+	+	–
Agosto 3,36 *0,82*	–	+	+	+	+	
Luglio 4,54 *0,84*	+	+	–	+		
Giugno 4,72 *0,85*	+	+	–			
Maggio 4,73 *0,78*	+	+				
Aprile 3,59 *0,79*	+					

Tabella 4: valori (log base 2) degli indici di diversità (in tondo) e di *evenness* relativi ai mesi di raccolta del 1990 nella stazione 9.

	Marzo 3,19 *0,76*	*Maggio* 4,15 *0,80*	*Giugno* 4,09 *0,84*	*Luglio* 3,89 *0,83*
Ottobre 3,01 *0,91*	–	+	+	+
Luglio 3,89 *0,83*	+	–	–	
Giugno 4,09 *0,84*	+	–		
Maggio 4,15 *0,80*	+			

Dal confronto dei valori ottenuti si può affermare che le stazioni 2, 4 e 5 costituiscono un blocco a diversità più elevata rispetto alle rimanenti, come già appare evidente dall'andamento delle curve di k-dominanza. La stazione 2 presenta anche il valore più elevato dell'indice di Margalef. Questo carattere di più marcata «naturalità» per la stazione 2 non è probabilmente dovuto ad una maggiore stabilità dell'ambiente, ma ad una minore pressione antropica rispetto alle altre aree di raccolta. Va però segnalato che negli ultimi due anni del periodo di campionamento la stazione è stata pesantemente interessata dagli scavi archeologici relativi al cosiddetto «Edificio 2», durante i quali il tappeto erboso è stato completamente asportato su una considerevole superficie. Il disturbo in genere provocato dalle attività agricole sulla diversità del popolamento è provato anche dai valori molto bassi dell'indice di diversità di Shannon per le tre stazioni più intensamente sfruttate (3-7-8).

Allo scopo di evidenziare l'evoluzione stagionale del popolamento, è stato inoltre condotto un confronto tra i diversi mesi di raccolta del 1990, anno in cui tutte le stazioni sono state indagate con regolarità per l'intera stagione. Anche in questo caso prima di calcolare gli indici di Shannon abbiamo tracciato le curve di k-dominanza, separando la stazione 9 (Fig. 5.2) dal complesso delle stazioni 1-8 (Fig. 5.1). Dall'andamento dei tracciati si osserva, come prevedibile, una maggiore dominanza all'inizio della primavera e nella stagione tardo estiva-autunnale. Nelle tabelle 3-4 sono riportati i valori (log base 2) degli indici di diversità (in tondo) e di *evenness* (in corsivo), evidenziando i confronti possibili (+).

Con un ulteriore confronto sono state messe in evidenza le affinità tra le stazioni 1-8 da un punto di vista qualitativo. A questo scopo abbiamo utilizzato l'indice di Sørensen J= C/(A+B-C) e la cluster analysis secondo il metodo WPGMA, dove C sono le specie comuni alle due stazioni messe a confronto, A le specie esclusive della prima stazione e B le specie esclusive della seconda stazione. I risultati vengono presentati nel dendrogramma in Fig. 6.1 a sinistra. Dall'analisi dei risultati si può rilevare che le stazioni 6; 5; 2, che rappresentano i prati non gestiti a foraggio, presentano una composizione crisomelidologica simile, mentre piuttosto differente risulta il popolamento dei prati 7; 8; 4, sottoposti, con maggiore o minore regolarità, alla pratica dello sfalcio. Le stazioni 3 e 1, pure falciate ma associate al cluster dei prati naturali, risentono probabilmente della vicinanza con la stazione 2 (poche decine di metri, in linea d'aria). L'influenza dell'azione antropica è messa ancor più in evidenza dall'indice di Sokal Michener, (Fig.6.1 a destra), che permette di separare in due cluster distinti i prati i prati «naturali» e quelli regolarmente falciati.

Risultati nel complesso analoghi si ottengono con l'analisi delle componenti principali (PCA). In particolare utilizzando soltanto le specie frequenti (almeno 20 esemplari raccolti nel complesso delle stazioni) si ottiene ancora una volta una netta separazione del complesso 6; 5; 2 (Fig. 6.2). La prima componente principale della variazione (asse 1, orizzontale) sembrerebbe in questo caso identificabile con la tendenza alla ripresa della copertura boschiva nelle stazioni non più gestite a foraggio (varie specie legate ad essenze arboree o arbustive presentano una elevata correlazione positiva con tale componente).

Interessante risulta il confronto tra il dendrogramma ottenuto con l'indice di Sørensen e quello ottenuto utilizzando l'indice multistato «percent similarity» sulla struttura del popolamento vegetale (Banfi, Galasso e Sassi, in questo stesso volume), riportato in Fig. 7. I due dendrogrammi, pur presentando affinità nell'associare alcune coppie di stazioni (7-8; 1-3; 6-5), differiscono però per una serie di elementi, fra cui, in botanica, l'isolamento delle stazioni 6-5 rispetto alle rimanenti. Queste differenze possono essere messe in relazione con fattori biologici quali la mobilità degli insetti e la polifagia di molte specie di crisomelidi, che rendono in effetti improbabile una completa sovrapposizione dei risultati.

Analisi faunistica

Viene di seguito riportato l'elenco ragionato delle 152 specie censite durante le raccolte. Ad esse possono essere aggiunti *Cryptocephalus (s. str) cordiger* (Linnaeus, 1758) e *Cryptocephalus (s.str.) octopunctatus* Scopoli che, benchè non reperiti nel corso del presente studio, furono segnalati per il monte Barro da Burlini (1955). Per quanto riguarda il genere *Asiore-*

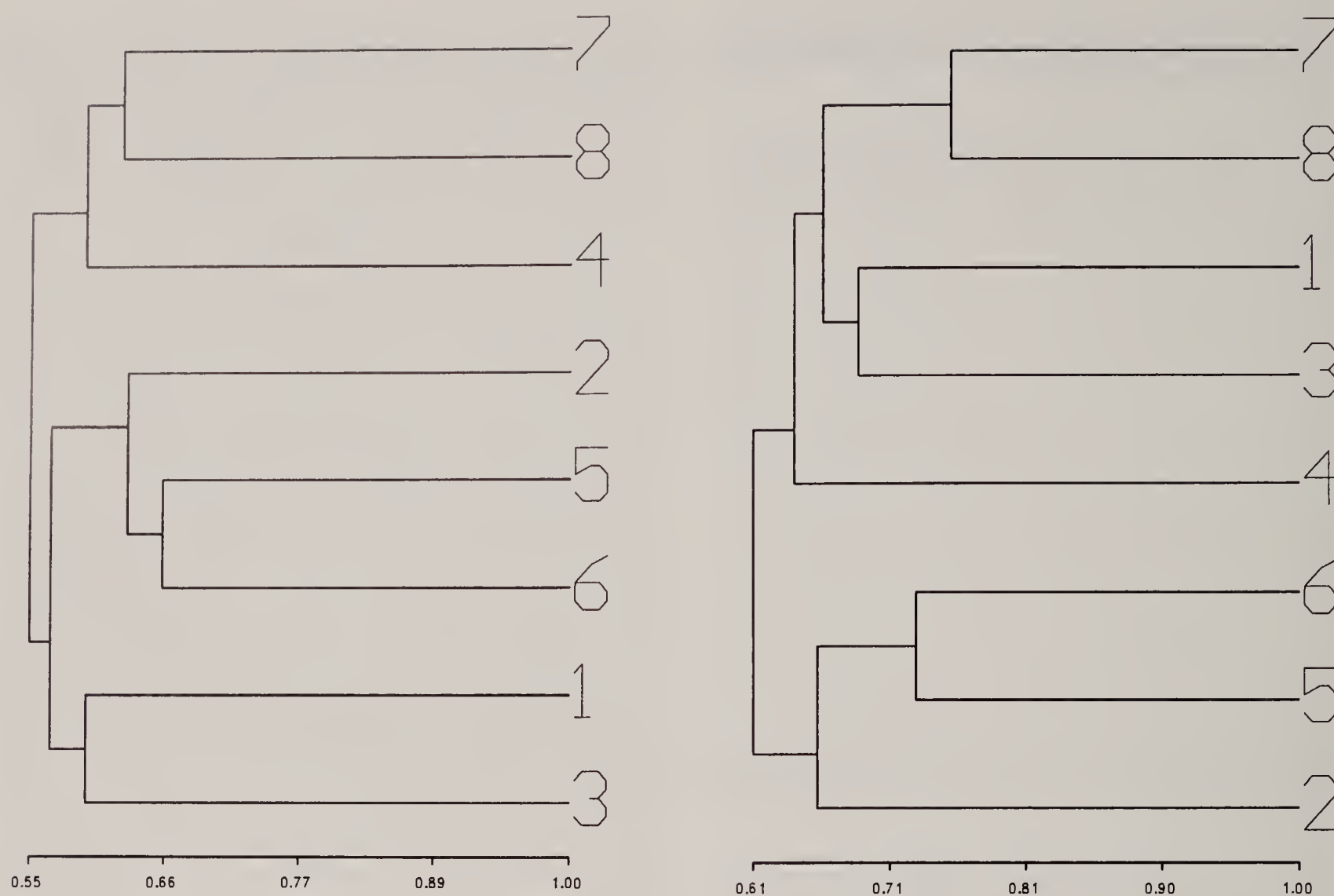



Fig. 6.1 - Dendrogrammi di similarità tra le stazioni 1-8 basati sui campionamenti dei Crisomelidi. A sinistra: indice di Sørensen + WPGMA. A destra: indice di Sokal-Michener + WPGMA.

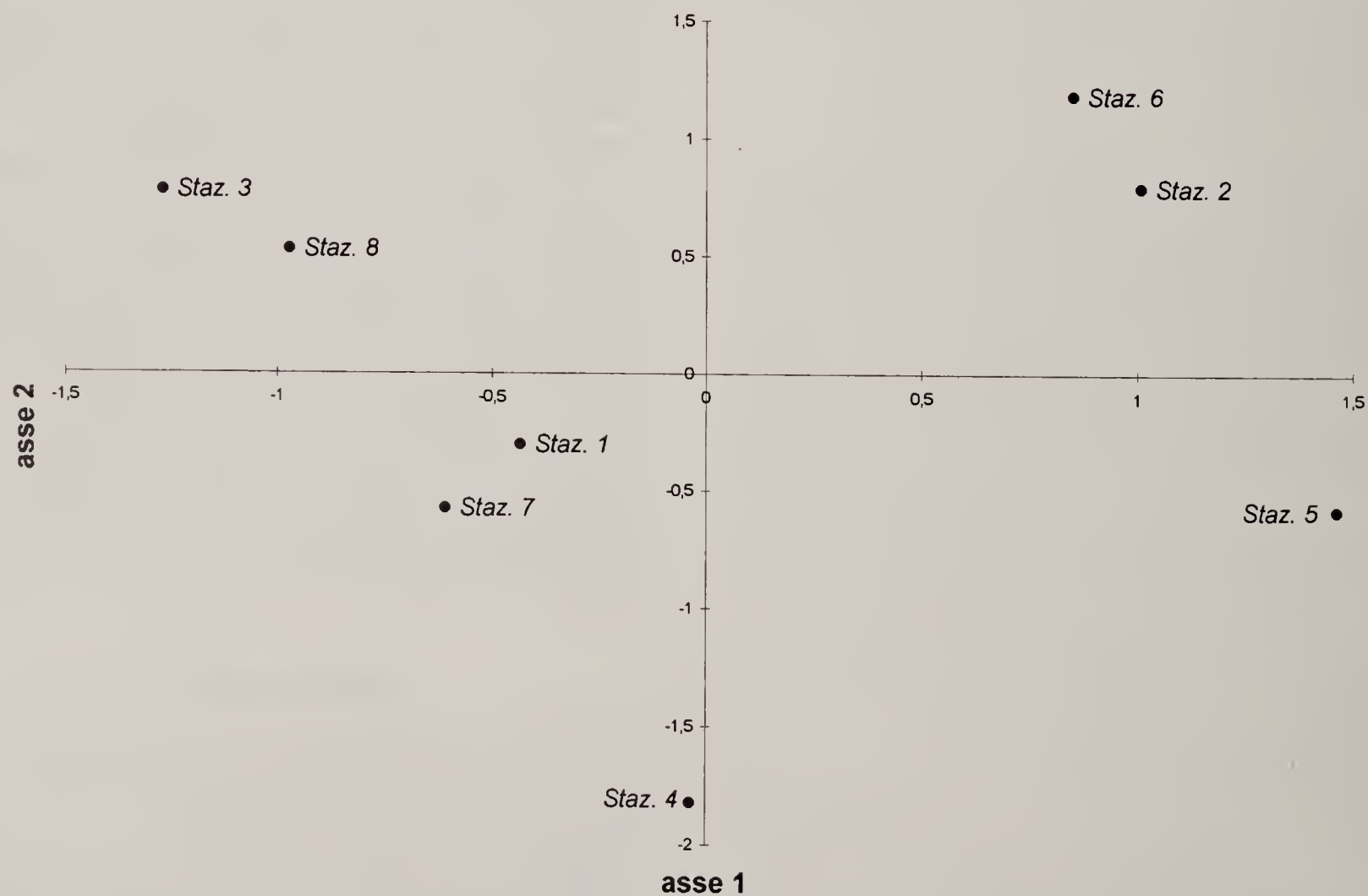



Fig. 6.2 - Confronto delle stazioni 1-8 mediante analisi delle componenti principali.

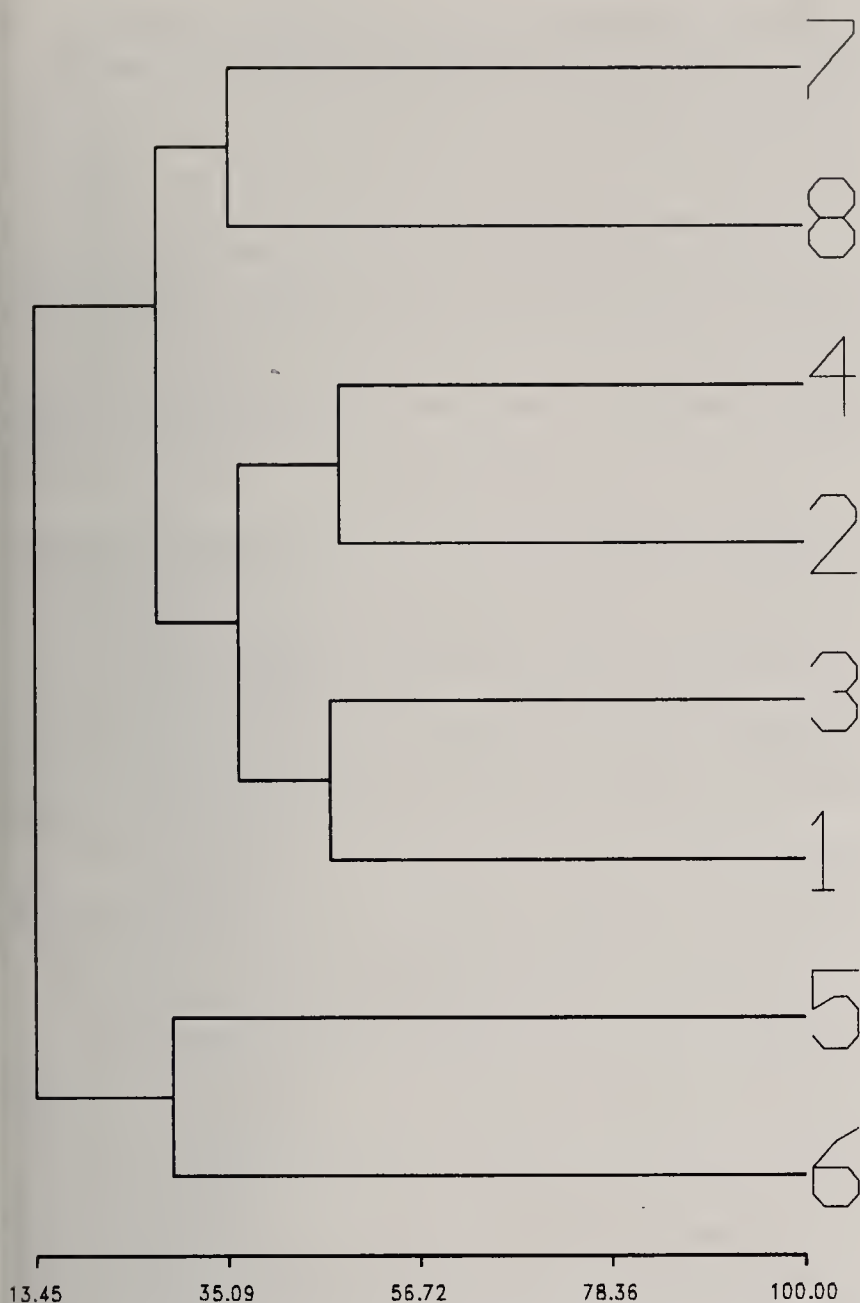



Fig. 7 - Dendrogramma di similarità tra le stazioni 1-8 basato sui rilievi botanici (Percent similarity + WPGMA).

stia Jacob. occorre osservare che recentemente esso è stato messo in sinonimia di *Neocrepidodera* Heiktgr. (Konstantinov & Vandenberg, 1996); siamo venuti a conoscenza di questo lavoro quando non ci era più possibile apportare la modifica.

Plateumaris rustica (Kunze, 1818)
Corotipo: Paleartico (PAL).
Presenza in Italia: regioni settentrionali.
Piante ospiti: *Cladium mariscus*, *Carex*.

Oulema duftschmidi (Redtenbacher, 1874)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: da definire.
Piante ospiti: Poacee coltivate e spontanee.

Crioceris duodecimpunctata duodecimpunctata (Linnaeus, 1758)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutta la Penisola, Sardegna, Sicilia.
Piante ospiti: *Asparagus*. Raccolta in Monte Barro su *Asparagus tenuifolius*.

Lilioceris lilii lilii (Scopoli, 1763)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta la Penisola, Sardegna, Sicilia.
Piante ospiti: *Lilium*, *Fritillaria*, *Convallaria*, *Polygonatum*. Raccolta in Monte Barro su *Lilium martagon*.

Lilioceris merdigera (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: comune nelle regioni settentrionali e centrali, molto più rara al Sud e probabilmente localizzata su massicci montuosi (Ruffo, 1964).
Piante ospiti: *Convallaria*, *Polygonatum*, *Lilium*, *Allium*. Causa danni, come la specie precedente, a liliacee coltivate. Raccolta in Monte Barro su *Polygonatum multiflorum*.
Note: Berti & Rapilly (1976), nella revisione delle specie paleartiche del genere *Lilioceris* indicano differenze morfometriche a sostegno della separazione specifica di *L. merdigera* da *L. schneideri* Weise. In particolare segnalano (p. 46), in un diagramma di dispersione per le variabili lunghezza e larghezza del pronoto espresse in forma logaritmica: «...malgré les chevaulchements ... nous avons observé des zones de dispersion bien individualisées». Su due piccoli campioni di *L. merdigera* del Monte Barro (9 esemplari) e di *L. schneideri* (Abruzzo, Prati di Tivo, 11 esemplari) abbiamo calcolato (in mm) i valori medi (m) e le rispettive deviazioni standard (s) della lunghezza e larghezza del pronoto. *L. schneideri* mostra effettivamente un pronoto più grande ((Lp) m = 1,88 s = 0,09; (lp) m = 1,95 s = 0,09), contro i corrispondenti valori di *merdigera* ((Lp) m = 1,74 s = 010; (lp) m = 1,85 s = 0,09). Sottoponendo i dati all'analisi della varianza per il confronto tra medie si ottengono differenze altamente significative (F=11,39) per le lunghezze e significative (F= 6,19) per le larghezze. Il rapporto lp/Lp non sembra invece avere importanza diagnostica, poiché il confronto tra le rette di regressione di lp su Lp (Fig.8) mediante l'analisi della covarianza indica una differenza non significativa (F=0,0667).

Labidistomis (s. str.) tridentata (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali.
Piante ospiti: *Corylus*, *Betula*, *Salix*, *Quercus*, *Spiraea*. Prevalentemente legata allo strato arbustivo, ma rinvenibile anche nei prati. In Monte Barro è stata raccolta su *Corylus avellana*.

Labidostomis (s. str.) longimana longimana (Linnaeus, 1761)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutta Italia.
Piante ospiti: Fabacee dei generi *Lotus* e *Trifolium*. Secondo Balachovski (1963) anche su Brassicacee selvatiche e cereali coltivati.

Lachnaia (s. str.) italica italica (Weise, 1882)
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutta la Penisola, Sicilia.
Piante ospiti: *Rubus*, occasionalmente *Quercus*. In Monte Barro è stata raccolta su *Rubus* sp.

Clytra (s. str.) quadripunctata (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta la Penisola.
Piante ospiti: *Betula*, *Crataegus*, *Salix*, *Quercus*, *Prunus* e vari alberi da frutto. In Monte Barro spesso raccolta su *Corylus avellana*.

Clytra (s. str.) appendicina Lacordaire, 1848
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutta la Penisola, Sicilia.
Piante ospiti: indicata in letteratura per diversi generi (*Salix*, *Rumex*, *Populus*, *Tamarix*, *Malus*).

Note: la posizione sistematica di *Clytra appendicina* è piuttosto controversa. Nella recente Checklist della fauna italiana (Biondi et al., 1994) è considerata sottospecie di *C. quadripunctata*. La convivenza delle due forme sul monte Barro sembrerebbe smentire questa interpretazione. In attesa di chiarimenti in merito preferiamo considerare specie distinta il taxon in questione.

Clytra (s. str.) laeviuscula (Ratzeburg, 1837)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta la Penisola, Sardegna.
Piante ospiti: *Salix*, *Prunus*, *Dorycnium*, *Fraxinus*. In Monte Barro è stata raccolta su *Salix cinerea* e *Ostrya carpinifolia*.

Smaragdina (s. str.) salicina (Scopoli, 1763)
Corotipo: Europeo (EUR).
Presenza in Italia: Penisola e Sicilia.
Piante ospiti: *Crataegus*, *Salix*. In Monte Barro è molto comune anche sulla vegetazione erbacea.

Smaragdina (s. str.) flavicollis (Charpentier, 1825)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali.
Piante ospiti: *Alnus glutinosa*.
Note: secondo Müller è specie moderatamente orofila.

Smaragdina (s. str.) aurita aurita (Linnaeus, 1767)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta la Penisola.
Piante ospiti: alberi e arbusti dei generi *Corylus*, *Crataegus*, *Betula*.

Smaragdina (s. str.) affinis (Illiger, 1794)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta la Penisola.
Piante ospiti: *Corylus*, *Quercus*, *Crataegus*. In Monte Barro in genere raccolta su *Corylus avellana*.

Coptocephala (s. str.) unifasciata unifasciata (Scopoli, 1763)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta la Penisola, Sicilia.
Piante ospiti: *Echinophora*, *Pastinaca*, *Daucus*, *Ferulago*.

Coptocephala (s. str.) scopolina kuesteri Kraatz, 1872
Corotipo: S-Europeo (SEU).
Presenza in Italia: Penisola, Sicilia.
Piante ospiti: Apiacee dei generi *Seseli* e *Daucus*.

Pachybrachis hieroglyphicus (Laicharting, 1781)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta la Penisola, Sicilia.
Piante ospiti: *Salix*, *Populus*, *Betula*. In Monte Barro esclusivamente raccolta su *Salix cinerea*.
Note: specie igrofila. Raccolte femmine gravide nella seconda metá di luglio.

Pachybrachis tessellatus tessellatus (Olivier, 1791)
Corotipo: S-Europeo (SEU).
Presenza in Italia: Penisola, Sicilia.
Piante ospiti: *Quercus*, *Salix*, *Corylus*, *Erica*.
Note: Specie xerofila.

Cryptocephalus (Homalopus) loreyi Solier, 1836
Corotipo: S-Europeo (SEU).
Presenza in Italia: diffuso su tutta la Penisola.
Piante ospiti: specie polifaga, legata allo strato arboreo-arbustivo. Fagacee, Corilacee, Rosacee.

Cryptocephalus (Homalopus) coryli (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).

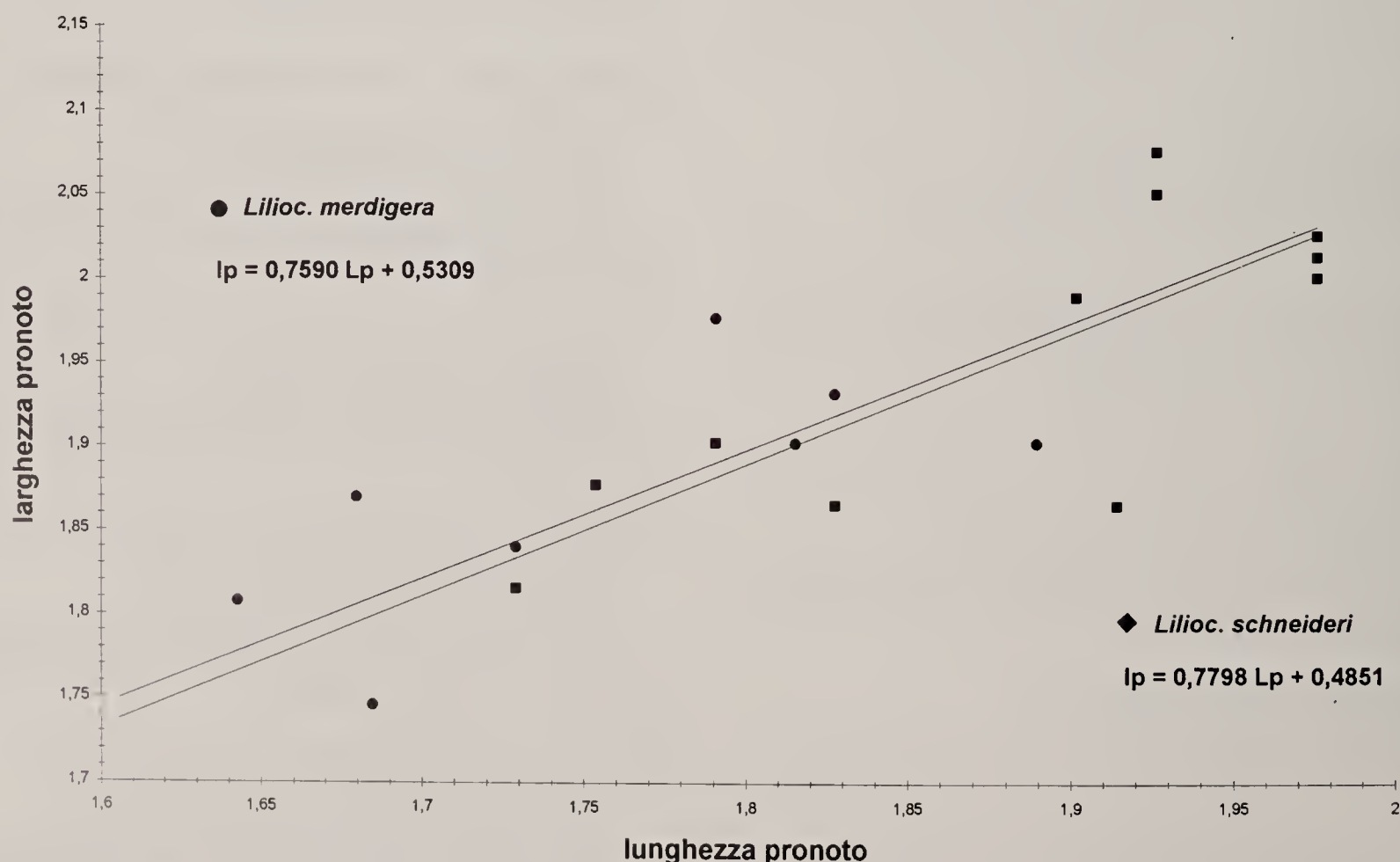



Fig. 8 - Variabilità delle dimensioni del pronoto in *Lilioceris merdigera* e *L. schneideri* (valori in millimetri).

Presenza in Italia: regioni settentrionali e centrali.
Piante ospiti: specie polifaga, legata allo strato arbustivo; Betulacee, Corilacee, Salicacee, Oleracee (*Fraxinus*), Rosacee. Gli esemplari furono raccolti su *Corylus avellana* e *Quercus pubescens*.

Cryptocephalus (s. str.) primarius Harold, 1872
Corotipo: specie a gravitazione S-Europea (SEU).
Presenza in Italia: regioni settentrionali e centrali.
Piante ospiti: specie polifaga; generalmente indicata su Corilacee, Salicacee, Fagacee; Bedel (1901) la ritiene invece legata al tappeto erboso. Da noi è stata sempre raccolta sfalciando i prati.

Cryptocephalus (s. str.) bimaculatus Fabricius, 1781
Corotipo: Mediterraneo (MED), noto soltanto per l'Italia, Francia meridionale e Marocco.
Presenza in Italia: regioni settentrionali e centrali, Campania, Calabria (Sila, Cotronei: inedito).
Piante ospiti: specie polifaga, indicata su Fabacee e Lamiacee; frequenta prevalentemente lo strato erbaceo e i bassi arbusti.
Note: elemento xerofilo, non molto comune.

Cryptocephalus (s. str.) trimaculatus Rossi, 1790
Corotipo: S-Europeo (SEU).
Presenza in Italia: diffuso in tutta la Penisola.
Piante ospiti: specie polifaga; Fagacee, Rosacee, Salicacee, Anacardiacee (*Pistacia*); presente anche sul tappeto erboso.

Cryptocephalus (s. str.) bipunctatus bipunctatus (Linnaeus, 1758)
Corotipo: Paleartico (PAL).
Presenza in Italia: diffuso in tutta la Penisola.
Piante ospiti: specie polifaga ad ampio spettro, legata allo strato arbustivo-arboreo. Indicata su Salicacee, Betulacee, Corilacee, Fagacee, Rosacee, Fabacee.
Note: Burlini (1955) ritiene la ab. *sanguinolentus* più comune della forma tipica sul territorio italiano. Sul Monte Barro questa variazione cromatica è invece decisamente rara.

Cryptocephalus (s. str.) sericeus zambanellus (Marseul, 1875)
Corotipo: S-Europeo (SEU).
Presenza in Italia: presente in tutta la Penisola.
Piante ospiti: specie polifaga, ma con tendenza all'oligofagia; Asteracee, Ranuncolacee, Boraginacee. Quest'ultima indicazione (Roubal, 1941) richiederebbe ulteriori conferme. Raccolta prevalentemente su *Inula hirta* e *Geranium sanguineum*.

Cryptocephalus (s. str.) transiens Franz, 1949
Corotipo: S-Europeo (SEU).
Presenza in Italia: regioni settentrionali.
Piante ospiti: specie polifaga, legata al tappeto erboso. *Hypericum*, *Ranunculus*, *Anthyllis*, *Genista*, *Hieracium*, *Leontodon*, *Hypochoeris*, *Helichrysum*, *Taraxacum*, *Centaurea*. Accertata la frequentazione di fiori di colore giallo, indipendentemente dalla famiglia di appartenenza. Tale comportamento è presente anche in specie affini (*C. hypochaeridis*, *sericeus*, *aureolus*, *barii*). Raccolta sul Monte Barro su diverse piante, tra cui *Ranunculus* spp., *Ruta graveolens*, *Lotus corniculatus*, *Genista tinctoria*.

Cryptocephalus (s. str.) nitidus (Linnaeus, 1758)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: presente in tutta la Penisola.
Piante ospiti: specie polifaga e legata allo strato arboreo-arbustivo; Fagacee, Corilacee, Betulacee, Rosacee. Prevalentemente raccolto su *Quercus* sp. e *Corylus avellana*.

Cryptocephalus (s. str.) janthinus Germar, 1824
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: presente in tutta la Penisola, Corsica e Sardegna.
Piante ospiti: legata ad ambienti umidi, polifaga ad ampio spettro; Poacee (*Phragmites*), Betulacee, Litracee, Salicacee.

Cryptocephalus (s. str.) parvulus parvulus Müller, 1776
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: presente in tutta la Penisola, Corsica e Sardegna.
Piante ospiti: specie polifaga, legata allo strato arbustivo-arboreo; Betulacee, Salicacee, Fagacee, Corilacee, Rosacee.

Cryptocephalus (s. str.) marginatus Fabricius, 1781
Corotipo: Europeo (EUR).
Presenza in Italia: tutta la Penisola.
Piante ospiti: essenze arbustive e arboree dei generi *Betula, Quercus, Salix, Populus, Sorbus, Rubus.*

Cryptocephalus (s. str.) moraei (Linnaeus, 1758)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: diffuso in tutta la Penisola e isole maggiori.
Piante ospiti: specie oligofaga, infeudata al genere *Hypericum* (Guttifere); popola il tappeto erboso.

Cryptocephalus (s. str.) flavipes Fabricius, 1781
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: diffuso in tutta la Penisola, Sicilia e Sardegna (P. Conte, dato inedito).
Piante ospiti: specie polifaga ad ampio spettro, prevalentemente legata allo strato arbustivo-arboreo; Salicacee, Betulacee, Fagacee, Corilacee, Cistacee. Presente anche sul tappeto erboso. Tra le essenze frequentate sul Monte Barro furono registrati: *Ostrya carpinifolia*, *Corylus avellana*, *Rubus* sp., *Geranium sanguineum*.
Note: per questa specie, essendo disponibile un numero piuttosto elevato di esemplari raccolti, è stata determinata la sex-ratio sui 167 individui provenienti da quindici diversi campionamenti, distribuiti su tre anni di raccolte in periodi compresi tra la seconda metà di maggio e la prima metà di luglio. I risultati rivelano la presenza di 67 maschi e 100 femmine, con uno scostamento significativo dal rapporto di 1:1 per il periodo studiato secondo il test del chi quadrato.

Cryptocephalus (s. str.) signatifrons Suffrian, 1847
Corotipo: S-Europeo (SEU).
Presenza in Italia: Penisola.
Piante ospiti: specie oligofaga, legata allo strato arbustivo. *Quercus*, *Corylus*. Sul Monte Barro generalmente raccolto sul nocciolo, ne è stata registrata la presenza anche su *Quercus pubescens* e *Ostrya carpinifolia*.

Cryptocephalus (s. str.) turcicus Suffrian, 1847
Corotipo: S-Europeo (SEU).

Presenza in Italia: Penisola, Sicilia, Sardegna.
Piante ospiti: specie xerofila e probabilmente oligofaga. *Quercus*, *Pistacia*. Quest'ultimo dato, derivante dalle segnalazioni di vecchi Autori, meriterebbe conferma. Generalmente raccolto sul Monte Barro su *Corylus avellana* e *Quercus pubescens*.

Cryptocephalus (Burlinius) bilineatus (Linnaeus, 1767)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e centrali.
Piante ospiti: Asteracee, Dipsacacee, Campanulacee. Secondo Suffrian anche su Plumbaginacee (*Statice*).

Cryptocephalus (Burlinius) elegantulus Gravenhorst, 1807
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e centrali.
Piante ospiti: specie polifaga legata allo strato erboso. Asteracee, Campanulacee, Geraniacee, Lamiacee. Elemento tendenzialmente xerofilo.

Cryptocephalus (Burlinius) strigosus Germar, 1823
Corotipo: S-Europeo (SEU).
Presenza in Italia: regioni peninsulari, fino alla Campania.
Piante ospiti: specie tendenzialmente oligofaga. *Thymus*, *Alnus*. Quest'ultimo dato, meriterebbe conferma.

Cryptocephalus (Burlinius) ocellatus Drapiez, 1819
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: Penisola, Sardegna, Sicilia.
Piante ospiti: segnalata su *Salix*, *Populus*, *Corylus*, *Quercus*, *Betula*, *Alnus*, *Ulmus*, *Mentha*, *Melissa*. Specie sicuramente polifaga, e legata allo strato arboreo-arbustivo. Le catture su essenze erbacee sono probabilmente accidentali.

Cryptocephalus (Burlinius) labiatus (Linnaeus, 1761)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Penisola, Sicilia.
Piante ospiti: specie polifaga ad ampio spettro, prevalentemente legata allo strato arbustivo, ma frequentemente raccolta anche sul tappeto erboso. *Betula*, *Alnus*, *Salix*, *Quercus*, *Populus*, *Fragaria*, *Vaccinium*.
Note: disponendo di un numero elevato di esemplari di questa specie, è stata determinata la sex-ratio su 110 individui raccolti in 16 date di campionamento, distribuite in quattro anni. I risultati evidenziano una fluttuazione stagionale (25 maschi e 12 femmine nelle raccolte del periodo maggio-giugno; 33 maschi e 40 femmine nelle raccolte di luglio), con uno scostamento significativo dal rapporto di 1:1 secondo il test del chi quadrato. La dissezione rivela peraltro che le femmine portano uova apparentemente mature (fino a 4-5 contemporaneamente), per tutto il periodo di attività. Vari esemplari furono osservati in copula nella prima metá di luglio.

Cryptocephalus (Burlinius) vittula Suffrian, 1848
Corotipo: la posizione tassonomica nei confronti di *C. pygmaeus* Fabr. è ancora da chiarire, in lavori di sintesi recenti (Warchalowski, 1991: 280; Gruev & Tomov, 1984: 176), il taxon è indicato come sinonimo di *C. pygmaeus*, mentre Kippenberg (1994: 39) lo considera specie distinta. Anche l'areale di distribuzione risulta pertanto mal definito. Sembra comunque presente in gran parte dell'Europa Meridionale, Asia Minore, Caucaso. Il taxon presente in Nord Africa è da sempre indicato come *C. pygmaeus*. Pertanto il corotipo può essere provvisoriamente indicato come S-Europeo (SEU).
Presenza in Italia: Penisola e Sicilia.
Piante ospiti: specie oligofaga, legata al tappeto erboso. Lamiacee dei generi *Origanum*, *Thymus*, *Satureja*, *Mentha*.

Cryptocephalus (Burlinius) fulvus fulvus Goeze, 1777
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Piante ospiti: specie polifaga ad ampio spettro, più frequente in genere sul tappeto erboso. Indicato in letteratura come legato a vari generi di Corilacee, Salicacee, Lamiacee, Asteracee, Fabacee, Guttifere, Geraniacee, Ericacee, Rubiacee, Apiacee (*Corylus*, *Populus*, *Salix*, *Thymus*, *Artemisia*, *Achillea*, *Vicia*, *Lotus*, *Trifolium*, *Hypericum*, *Geranium*, *Calluna*, *Galium*, *Pimpinella*, *Laserpitium*).

Cryptocephalus (Burlinius) pusillus Fabricius, 1777
Corotipo: Europeo (EUR).
Presenza in Italia: Penisola.
Piante ospiti: specie polifaga, legata allo strato arboreo arbustivo. *Populus*, *Alnus*, *Corylus*, *Quercus*, *Salix*, *Betula*. Sul Monte Barro è stata raccolta esclusivamente la forma cromatica *marshami* Weise. Relativamente comune all'inizio di luglio in località Pian Sciresa (Versante Est), su *Corylus avellana*.

Oomorphus concolor (Sturm, 1807)
Corotipo: C-Europeo (CEU).
Presenza in Italia: regioni centro settentrionali.
Piante ospiti: *Aegopodium podagraria*.
Note: specie moderatamente orofila.

Eumolpus asclepiadeus (Pallas, 1773)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e centrali.
Piante ospiti: *Vincetoxicum*, *Cynanchum*. Sul Monte Barro la specie è strettamente legata a *Vincetoxicum hirundinaria*.

Leptinotarsa decemlineata (Say, 1824)
Corotipo: Neartico; specie importata in Europa e rapidamente stabilizzata.
Presenza in Italia: tutta la Penisola, Sicilia.
Piante ospiti: Solanacee spontanee e coltivate. Secondo Balachovski (1963) può trovarsi occasionalmente anche su *Chenopodium*, *Sisimbrium*, e *Achillea*.

Chrysolina (Euchrysolina) graminis santonici (Contarini, 1847)
Corotipo: S-Europeo (SEU).
Presenza in Italia: Penisola.
Piante ospiti: questa specie è indicata da vari autori su Asteracee (*Thanacetum*, *Achillea*) e Lamiacee (*Lycopus*, *Stachys*). Bourdonnè e Doguet, che la raccolsero e la allevarono su *Mentha aquatica* e *M. pulegium*, ritengono che *Achillea* rappresenti solo un ospite occasionale degli adulti. Nella stazione in cui

fu raccolta, la osservammo varie volte, in riposo, sulla pagina superiore delle foglie di *Phragmites australis*.

Chrysolina (Erythrochrysa) polita (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta la Penisola, Sardegna, Sicilia.
Piante ospiti: Lamiacee (*Mentha*, *Melissa*, *Lycopus*, *Salvia*, *Origanum*, *Nepeta*, *Glechoma*).
Note: nel territorio studiato fu osservata la presenza di esemplari immaturi nella prima metá del mese di ottobre.

Chrysolina (Chrysomorpha) cerealis mixta (Kuester, 1844)
Corotipo: S-Europeo (SEU).
Presenza in Italia: regioni settentrionali e centrali.
Piante ospiti: indicati in letteratura diversi generi di Lamiacee (*Thymus*, *Rosmarinus*, *Satureja*, *Calamintha*). Secondo Ruffo (1938) potrebbe essere monofaga (*Thymus serpillum*).

Chrysolina (Minckia) oricalcia (Muller, 1776)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Penisola, Sicilia.
Piante ospiti: Apiacee (*Anthriscus*, *Chaerophyllum*, *Aegopodium*).

Chrysolina (Colaphodes) haemoptera (Linnaeus, 1758)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: Penisola e Sardegna, dubitativamente in Sicilia.
Piante ospiti: *Plantago*.

Chrysolina (Stichoptera) rossia (Illiger, 1802)
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutta la Penisola.
Piante ospiti: Scrofulariacee (*Linaria*).

Chrysolina (Chalcoidea) marginata marginata (Linnaeus, 1758)
Corotipo: Paleartico (PAL).
Presenza in Italia: regioni settentrionali.
Piante ospiti: *Achillea*, *Artemisia*, *Leucanthemum*.

Chrysolina (Fastuolina) fastuosa fastuosa (Scopoli, 1763)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Penisola.
Piante ospiti: *Galeopsis*, *Lamium*. Sul Monte Barro fu raccolta su *Lamium maculatum* e *Galeopsis pubescens*.

Gastrophysa viridula (De Geer, 1775)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni settentrionali.
Piante ospiti: *Rumex*, *Polygonum*, *Oxyria*, *Rheum*.

Phaedon (s. str.) cochleariae (Fabricius, 1792)
Corotipo: Paleartico (PAL).
Presenza in Italia: penisola e, dubitativamente, Sardegna.
Piante ospiti: Brassicacee dei generi *Nasturtium*, *Rorippa*, *Armoracia*, *Brassica*, *Sinapis*, ed inoltre su *Veronica beccabunga* (Scrofulariacee). Presente a volte su Brassicacee coltivate.
Note: specie igrofila.

Hydrothassa marginella (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali.
Piante ospiti: Ranuncolacee dei generi *Ranunculus* e *Caltha*.

Plagiodera versicolora (Laicharting, 1781)
Corotipo: Olartico (OLA), presente anche in India e Taiwan (Gruev e Tomov, 1986).
Presenza in Italia: tutte le regioni.
Piante ospiti: *Salix*, *Populus*. Fu raccolta sul Monte Barro su *Salix cinerea*.

Chrysomela (Chrysomela) populi Linnaeus, 1758
Corotipo: Asiatico-Europeo (ASE), presente anche in India (Gruev e Tomov, 1986).
Presenza in Italia: tutte le regioni.
Piante ospiti: *Populus*, *Salix*. Sul Monte Barro fu raccolto su polloni di *Populus tremula*.

Timarcha (Timarcha) nicaeensis Villa, 1835
Corotipo: S-Europeo (SEU).
Presenza in Italia: regioni settentrionali.
Piante ospiti: Rubiacee del genere *Galium*.

Galerucella (Galerucella) nimphaeae (Linnaeus, 1758)
Corotipo: Olartico (OLA).
Presenza in Italia: Penisola.
Piante ospiti: indicati diversi generi di piante acquatiche o di luoghi umidi (*Nimphaea*, *Nuphar*, *Potamogeton*, *Polygonum*, *Rumex*, *Sagittaria*, *Potentilla*).

Galerucella (Galerucella) lineola lineola (Fabricius, 1781)
Corotipo: Paleartico (PAL).
Presenza in Italia: Penisola, Sicilia e Sardegna.
Piante ospiti: indicate in letteratura essenze arboreo arbustive (*Alnus*, *Salix*, *Corylus*) ed erbacee (*Lysimachia* e *Rumex*).

Galerucella (Neogalerucella) pusilla (Duftschmid, 1825)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Penisola.
Piante ospiti: *Lythrum*, dubitativamente anche *Stachys*, *Veronica*. Sul Monte Barro costantemente raccolta su *Lythrum salicaria*.
Note: specie igrofila.

Galeruca (Galeruca) tanaceti (Linnaeus, 1758)
Corotipo: Paleartico (PAL), introdotta anche in N. America secondo Gruev e Tomov (1986).
Presenza in Italia: Penisola, Sicilia.
Piante ospiti: Asteracee (*Achillea*, *Chrysanthemum*), Brassicacee (*Cardamine*), Cariofillacee (*Cerastium*).
Note: nella prima metá di ottobre furono raccolte femmine con uova.

Galeruca (Galeruca) pomonae (Scopoli, 1763)
Corotipo: Asiatico-Europeo (ASE), introdotta e stabilizzata negli USA (Lopatin, 1977).
Presenza in Italia: Penisola, Sardegna, Sicilia.
Piante ospiti: Asteracee, Cariofillacee, Lamiacee, Crucifere, Dipsacacee (*Centaurea*, *Scabiosa*, *Cirsium*, *Leontodon*, *Phlox*, *Salvia*, *Capsella*, *Knautia*).

Exosoma lusitanicum (Linnaeus, 1767)
Corotipo: W-Mediterraneo (WME).
Presenza in Italia: Penisola, Sardegna, Sicilia.
Piante ospiti: *Centaurea*, *Senecio*, *Vincetoxicum*, *Vitis*, Cucurbitacee. Specie polifaga ad ampio spettro; le larve rodono i bulbi di Liliacee e Amarillidacee.

Calomicrus circumfusus (Marsham, 1802)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Penisola.
Piante ospiti: *Genista*, *Spartium*. In Monte Barro prevalentemente su *Genista tinctoria*.

Luperus longicornis (Fabricius, 1781)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali.
Piante ospiti: *Alnus*, *Corylus*, *Salix*, *Betula*. Sul Monte Barro fu osservato su *Corylus avellana* e *Crataegus* sp.
Note: vari immaturi raccolti tra la seconda metá di aprile e la prima di maggio.

Luperus flavipes (Linnaeus, 1767)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali, Toscana.
Piante ospiti: *Alnus*, *Betula*, *Salix*, *Corylus*, *Ostrya*. Raccolto in Monte Barro su *Quercus pubescens* e *Crataegus* sp.

Luperus leonardii Fogato, 1978
Corotipo: S-Europeo (SEU).
Presenza in Italia: Penisola.
Piante ospiti: *Corylus*, *Ulmus*.

Phyllotreta vittula (Redtenbacher, 1849)
Corotipo: Paleartico (PAL). La specie è presente anche nella regione Neartica probabilmente per effetto di importazione.
Presenza in Italia: Italia peninsulare.
Piante ospiti: Poacee, Brassicacee, occasionalmente Asteracee, Chenopodiacee e Ciperacee. L'insetto è ampiamente diffuso negli arrenatereti e mesobrometi del Monte Barro anche in assenza di brassicacee.

Phyllotreta nemorum (Linneo, 1758)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Piante ospiti: Brassicacee.

Phyllotreta striolata (Fabricius, 1801)
Corotipo: Paleartico (PAL). La specie è presente anche nelle regioni Neartica, Afrotropicale e Orientale probabilmente per effetto di importazione.
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Lazio, Abruzzo, Campania.
Piante ospiti: Brassicacee.

Phyllotreta ochripes (Curtis, 1837)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale e centrale, Puglia, Sicilia.
Piante ospiti: Brassicacee; sul Monte Barro *Alliaria petiolata*.

Phyllotreta aerea Allard, 1859
Corotipo: Europeo-Mediterraneo (EUM). La specie è presente anche nella regione Neartica probabilmente per effetto di importazione.
Presenza in Italia: tutte le regioni.
Piante ospiti: Brassicacee, Resedacee.

Aphthona cyparissiae (Koch, 1803)
Corotipo: Europeo (EUR).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Trentino-Alto Adige, Lombardia, Val d'Aosta, Abruzzo.
Piante ospiti: Euforbiacee del genere *Euphorbia*.

Aphthona lutescens (Gyllenhal, 1808)
Corotipo: Turanico-Europeo (TUE)
Presenza in Italia: tutte le regioni.
Piante ospiti: Litracee, Lamiacee (?), Rosacee.
Note biologiche: *A. lutescens* è caratteristica di fragmiteti, dove vive su *Lythrum salicaria*, o di molinieti, dove vive su *Filipendula ulmaria*; Doguet (1994: 127) asserisce di averla trovata in numero anche su *Rubus* ma sul Monte Barro l'insetto non sembra frequentare questa pianta: è comune nella palude di Ca' di Sala e assente nelle stazioni all'interno del parco, se si esclude un unico reperto in Val di Faè, che riteniamo del tutto accidentale.
Note sistematiche: alla varietà *praeclara* Weise, che occupa la parte orientale dell'areale, alcuni autori attribuiscono valore di sottospecie.

Aphthona pygmaea pygmaea Kutschera, 1861
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni.
Piante ospiti: Euforbiacee del genere *Euphorbia*.
Note biologiche: Perner (1996: 247, 253-254) la considera specie xerotermofila; in praterie aride (teucrio-seslerieti) dell'ex Germania orientale ha riscontrato la presenza di individui immaturi da fine luglio a fine agosto e di femmine con uova da aprile a giugno; secondo questo autore gli adulti sono attivi fino all'inizio di novembre e ricompaiono in aprile dopo aver superato l'inverno.
Note sistematiche: è generalmente ammessa l'esistenza di una sottospecie (*orientalis* Mulsant & Rey) nelle regioni sud-orientali del Mediterraneo, caratterizzata dalla notevole finezza della punteggiatura elitrale.

Aphthona venustula venustula Kutschera, 1861
Corotipo: Europeo (EUR).
Presenza in Italia: ssp. tipica: Italia settentrionale e centrale, Campania, Basilicata, Puglia; ssp. *attica* Weise, 1890: Sicilia.
Piante ospiti: Euforbiacee del genere *Euphorbia*.
Note biologiche: sul Monte Barro i maschi, molto comuni in maggio, sembrano diventare più rari rispetto alle femmine nel mese successivo. Abbiamo rilevato la presenza di femmine con uova in giugno e un maschio non del tutto maturo è stato raccolto alla fine di agosto. Secondo Perner (1996: 254, 257) gli adulti, in praterie aride dell'ex Germania orientale, sono attivi da aprile (dopo lo svernamento) all'inizio di luglio e compaiono femmine con uova da aprile a giugno.

Aphthona coerulea (Geoffroy, 1785)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: regioni settentrionali e centrali, Campania, Basilicata, Puglia, Sicilia, Sardegna.
Piante ospiti: specie monofaga, sembra vivere esclusivamente su *Iris pseudacorus*.
Note biologiche: *A. coerulea* è un elemento carat-

teristico di ambienti palustri; è comunissima nella palude di Ca' di Sala, mentre la sua presenza, occasionalmente riscontrata, in altre stazioni è da ritenersi del tutto accidentale.

Aphthona herbigrada (Curtis, 1837)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Piante ospiti: Cistacee del genere *Helianthemum*; sul Monte Barro soprattutto *Helianthemum nummularium*.
Note biologiche: per quanto l'insetto sul Monte Barro sia stato raccolto anche in primavera, diventa molto comune nella seconda metà dell'estate e all'inizio dell'autunno. Individui visibilmente immaturi compaiono già alla fine di giugno ma si trovano numerosi soprattutto nei mesi di luglio e agosto (verso la fine di questo mese rappresentano ancora circa il 10% degli esemplari raccolti). Il rapporto maschi/femmine, calcolato su 2 campioni, ha fornito i seguenti valori: 0,88 (25.8.1992, dimensione del campione: 150 esemplari; 0,93 (25.9.1992, dimensione del campione: 108 esemplari). Perner (1996: 253, 255), in praterie aride dell'ex Gemania orientale, ha osservato la presenza di femmine con uova da fine agosto a fine ottobre.

Aphthona ovata Foudras, 1860
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale, Toscana, Lazio, Calabria, Sicilia.
Piante ospiti: Euforbiacee del genere *Euphorbia*. Sul Monte Barro comune soprattutto su *Euphorbia dulcis*, nei boschi della Val di Faè.
Note biologiche: in un campione del 26 settembre è stata riscontrata la presenza di un maschio e di una femmina leggermente immaturi.

Aphthona atrovirens (Foerster, 1849)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Friuli-Venezia Giulia, Trentino-Alto Adige, Lombardia, Piemonte, Toscana, Marche, Lazio, Abruzzo, Molise (Matese: M.te Miletto, dato inedito), Calabria.
Piante ospiti: secondo Weise (1893: 1137) *Euphorbia cyparissias* L., secondo altri autori (Mohr, 1966: 217; Warchalowski: 1978: 41; Biondi, 1990: 114) *Helianthemum* e *Linum*; sul Monte Barro quasi tutti gli esemplari sono stati raccolti, insieme ad *Aphthona ovata*, su *Euphorbia dulcis*, in prati della Val di Faè, ai margini di boschi dell'alleanza *Carpinion betuli*.

Longitarsus (s. str.) pellucidus (Foudras, 1860)
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM). La specie è presente anche nella regione Neartica, probabilmente per effetto di importazione.
Presenza in Italia: tutte le regioni.
Piante ospiti: Convolvulacee, soprattutto genere *Convolvulus*.

Longitarsus (s. str.) succineus succineus (Foudras, 1860)
Corotipo: Paleartico (PAL). La specie è presente anche nella regione Neartica probabilmente per effetto di importazione.
Presenza in Italia: tutte le regioni.
Piante ospiti: Convolvulacee, Plantaginacee, Lamiacee, Boraginacee, Asteracee.
Note biologiche: è probabile che l'insetto abbia uno sviluppo larvale primaverile, infatti sul Monte Barro gli adulti sono relativamente rari in maggio, mentre si riscontra una presenza massiccia di esemplari immaturi nei mesi di giugno e luglio e di femmine con uova in settembre. In un campione di 81 esemplari, raccolto il 18.6.1991 e formato interamente da individui più o meno immaturi, il rapporto maschi/femmine ha fornito il valore 1,25. Perner (1996: 252-254), basandosi sul comportamento della specie in praterie aride dell'ex Germania orientale, ritiene che nel *L. succineus* gli stadi di svernamento possano essere l'uovo, la larva o la pupa; egli ha osservato femmine con uova da fine giugno a fine agosto e individui immaturi dall'inizio di maggio alla fine di giugno.

Longitarsus (s. str.) noricus Leonardi, 1976
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Friuli-Venezia Giulia, Trentino-Alto Adige, Veneto, Lombardia e Piemonte.
Piante ospiti: Plantaginacee del genere *Plantago*, Lamiacee del genere *Salvia*, Asteracee.

Longitarsus (s. str.) rubiginosus (Foudras, 1860)
Corotipo: Sibirico-Europeo (SIE). La specie è presente anche nella regione Neartica probabilmente per effetto di importazione.
Presenza in Italia: Friuli-Venezia Giulia, Trentino Alto Adige, Lombardia, Piemonte, Toscana, Umbria, Lazio, Abruzzo, Puglia, Basilicata, Sardegna.
Piante ospiti: Convolvulacee con particolare preferenza per il genere *Calystegia*.

Longitarsus tabidus (Fabricius, 1775)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Piante ospiti: Scrofulariacee del genere *Verbascum*.

Longitarsus (s. str.) nigrofasciatus nigrofasciatus (Goeze, 1977)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Piante ospiti: Scrofulariacee dei generi *Verbascum* e *Scrophularia*.

Longitarsus (s. str.) foudrasi Weise, 1893
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Lombardia (prima segnalazione), Piemonte.
Piante ospiti: Scrofulariacee del genere *Verbascum*.
Note: l'insetto è stato trovato in due soli esemplari il 26.IX.92, lungo un sentiero che va da Galbiate verso la località di S. Michele.

Longitarsus (s. str.) lycopi (Foudras, 1860)
Corotipo: Turanico-Europeo-Mediterraneo (TEM). Questa specie penetra marginalmente anche nella regione Afrotropicale.
Presenza in Italia: tutte le regioni.
Piante ospiti: Lamiacee dei generi *Mentha* e *Lycopus*.
Note: questa specie è del tutto sporadica all'interno del parco, in quanto tipica di ambienti molto umidi; risulta invece comunissima nella palude a Cà di Sala.

Longitarsus* (*s. str.*) *obliteratus (Rosenhauer, 1847)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutta la Penisola.
Piante ospiti: Lamiacee. Sul Monte Barro sembra frequentare soprattutto i generi *Stachys*, *Thymus* e *Origanum*.
Note biologiche: Perner (1996: 251-252) lo ritiene specie xerotermofila; in praterie aride (Teucrio-Seslerieti) dell'ex Germania orientale segnala la presenza di femmine con uova da aprile a giugno e da settembre a novembre e di individui immaturi da luglio ad agosto. Sul Monte Barro abbiamo riscontrato la presenza di femmine con uova da fine marzo a fine maggio e raccolto individui immaturi in agosto, settembre e ottobre. Il rapporto maschi/femmine, calcolato su quattro campioni, ha fornito i seguenti valori: 1,83 (23.5.1991, dimensioni del campione: 34 esemplari); 0,54 (25.8.1992, dimensione del campione: 17 esemplari); 3,6 (25.9.1992, dimensione del campione: 23 esemplari); 0,54 (10.10.1990, dimensione del campione 17 esemplari).

Longitarsus* (*s. str.*) *salviae Gruev, 1975
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Lombardia, Puglia.
Piante ospiti: Lamiacee del genere *Salvia*.
Note biologiche: Perner (1996: 252-253) lo ritiene specie xerotermofila; in praterie aride (Teucrio-Seslerieti) dell'ex Germania orientale segnala la presenza di femmine con uova da aprile (immediatamente dopo lo svernamento) all'inizio di giugno. Sul Monte Barro abbiamo riscontrato la presenza di femmine con uova nei mesi di marzo, aprile e maggio e raccolto numerosi esemplari fortemente immaturi nei mesi di agosto e settembre. Il rapporto maschi/femmine, calcolato su 3 campioni, ha fornito i seguenti valori: 2 (10.VI.1991, dimensione del campione: 12 esemplari); 1,93 (25.8.1992, dimensione del campione: 41 esemplari); 1,13 (26.9.1992, dimensione del campione: 17 esemplari).

Longitarsus* (*s. str.*) *helvolus Kutschera, 1863
Corotipo: Cetroeuropeo (CEU).
Presenza in Italia: Friuli-Venezia Giulia, Lombardia, Liguria, Toscana, Calabria, Sicilia (?).
Piante ospiti: Lamiacee (*Teucrium chamaedrys*).
Note biologiche: Doguet (1993) scrive di averlo raccolto sempre in stazioni calde su terreni calcarei. Perner (1996: 249-250) lo ritiene specie xerotermofila; in praterie aride (Teucrio-Seslerieti) dell'ex Germania orientale egli ha riscontrato la presenza di femmine con uova da agosto a maggio e di individui immaturi da luglio a settembre. Sul Monte Barro è molto comune, soprattutto in settembre, nelle praterie cespugliate e con parziale affioramento roccioso che formano la stazione 6; nelle raccolte compaiono pochissimi esemplari immaturi. Il rapporto maschi /femmine, calcolato su due campioni, ha fornito i seguenti risultati: 0,36 (3.9.1991; dimensioni del campione: 15 esemplari; 0,20 (25.9.1992; dimensioni del campione: 73 esemplari).
Note sistematiche: tutte le citazioni di *Longitarsus membranaceus* Foudras per la fauna italiana sembrano riferirsi a questo taxon recentemente rivalutato da Doguet.

Longitarsus* (*s. str.*) *melanocephalus (De Geer, 1775)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: tutte le regioni.
Piante ospiti: Plantaginacee del genere *Plantago*.
Note biologiche: sono stati raccolti individui immaturi in giugno e nella seconda metà di settembre. Il rapporto maschi/femmine, calcolato su tre campioni, ha fornito i seguenti valori: 1,75 (15.6.1989, dimensione del campione: 11 esemplari); 1,83 (27.6.1989, dimensione del campione: 17 esemplari); 0,71 (30.3.1990, dimensione del campione: 29 esemplari).

Longitarsus* (*s. str.*) *niger (Koch, 1803)
Corotipo: Europeo (EUR).
Presenza in Italia: tutte le regioni.
Piante ospiti: Boraginacee (?), Plantaginacee del genere *Plantago*. Sul Monte Barro abbiamo raccolto questa specie in prati in cui erano presenti sia *Echium vulgare* che *Plantago lanceolata* ma non ci è stato possibile individuare con sicurezza la sua pianta ospite. Doguet (1994: 201) ha potuto riscontrare la presenza di numerosi esemplari di *L. niger* nell'atto di rodere foglie di *Plantago lanceolata* e questo dato biologico conferma la vicinanza sistematica di questo insetto con *L. melanocephalus* (De Geer).
Note biologiche: è stata riscontrata la presenza di esemplari immaturi alla fine di giugno.

Longitarsus* (*s. str.*) *exoletus (Linnaeus, 1758)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Friuli-Venezia Giulia, Trentino-Alto Adige, Lombardia (prima segnalazione), Liguria, Emilia-Romagna, Toscana, Lazio, Abruzzo, Campania, Puglia, Sicilia.
Piante ospiti: Boraginacee; sul M. Barro è stato raccolto solo su *Echium vulgare*.
Note sistematiche: gli esemplari raccolti sul M. Barro presentano in parte le caratteristiche cromatiche dalla forma tipica, in parte quelle della razza mediterranea *rufulus* (Foudras, 1860). Condividiamo l'opinione di Biondi (1990), che ritiene la ssp. *rufulus* una semplice forma cromatica, non sufficientemente distinta da poterle attribuire valore sistematico.
Note biologiche: secondo Müller (1953), il quale fa riferimento a un precedente lavoro di Buddeberg, l'insetto sverna nel terreno come larva, diventa immagine in primavera e depone le uova dalla fine di giugno a metà agosto; sul Monte Barro noi abbiamo trovato numerosi esemplari immaturi nel mese di giugno e femmine con uova da metà luglio all'inizio di ottobre.

Longitarsus* (*s. str.*) *lewisii (Baly, 1874)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Friuli-Venezia Giulia, Trentino-Alto Adige, Veneto, Lombardia, Piemonte, Valle d'Aosta, Emilia-Romagna.
Piante ospiti: Plantaginacee del genere *Plantago*; è noto un caso di allotrofia su *Mentha arvensis* (Leonardi & Doguet, 1990: 41).
Note biologiche: per quanto si trovi anche in primavera *L. lewisii* è un tipico insetto tardo-estivo autunnale; abbiamo raccolto femmine con uova all'inizio di aprile e a metà giugno, mentre esemplari immaturi compaiono in settembre. Il rapporto maschi/femmine, calcolato su 2 campioni, ha fornito i seguenti valori: 1,67 (13.9.1990, dimensione del campione: 32 esemplari); 1,10 (20.9.1989, dimensione del campione: 65 esemplari).

Longitarsus (s. str.) pratensis (Panzer, 1794)
Corotipo: Europeo-Mediterraneo (EUM). La specie è presente anche nella regione Neartica probabilmente per effetto di importazione.
Presenza in Italia: tutte le regioni.
Piante ospiti: Plantaginacee del genere *Plantago*.
Note biologiche: sono state raccolte femmine con uova a metà del mese di marzo. Il rapporto maschi/femmine, calcolato su tre campioni, ha fornito i seguenti risultati: 1,8 (14.3.1990, dimensione del campione: 42 esemplari); 1,71 (10.6.1991; dimensione del campione: 19 esemplari); 1,73 (20.9.1989, dimensione del campione: 71 esemplari).

Longitarsus (s. str.) longiseta Weise, 1889
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Friuli-Venezia Giulia, Trentino-Alto Adige, Lombardia, Piemonte.
Piante ospiti: Plantaginacee del genere *Plantago* e Scrofulariacee del genere *Veronica*.
Note biologiche: abbiamo riscontrato la presenza di individui immaturi all'inizio di agosto e nella seconda decade di settembre, e di femmine con uova dalla fine di maggio alla seconda decade di giugno. Alcuni campioni ricavati da raccolte effettuate nei mesi di marzo, giugno e settembre fanno credere che i maschi siano di norma più frequenti delle femmine, ma questa impressione non è confermata dall'esame di materiale proveniente da altre località (in un campione di 48 esemplari, in gran parte immaturi, raccolto in Val Vigezzo il 27.8.1971 la sex ratio è risultata 1,00).

Longitarsus nasturtii (Fabricius, 1972)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Trentino-Alto Adige, Lombardia, Piemonte, Toscana, Umbria, Lazio, Abruzzo, Calabria.
Piante ospiti: Boraginacee, soprattutto *Symphytum officinale*.
Note biologiche: *L. nasturtii* vive generalmente in ambienti piuttosto umidi; l'abbiamo rinvenuto esclusivamente nella palude di Ca' di Sala.

Longitarsus (s. str.) holsaticus (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Italia settentrionale e centrale, Campania.
Piante ospiti: Scrofulariacee dei generi *Veronica*, *Pedicularis* e *Gratiola*.

Longitarsus (s. str.) luridus (Scopoli, 1763)
Corotipo: Paleartico (PAL). La specie è presente anche nella regione Neartica probabilmente per effetto di importazione.
Presenza in Italia: tutte le regioni.
Piante ospiti: Ranuncolacee dei generi *Ranunculus* e *Clematis*, Boraginacee dei generi *Symphytum* e *Pulmonaria*, Lamiacee del genere *Clinopodium*, Plantaginacee del genere *Plantago*, Dipsacacee del genere *Succisa*, Scrofulariacee del genere *Rhinanthus*.
Note biologiche: abbiamo raccolto femmine con uova nella seconda metà di aprile e individui immaturi da metà giugno a metà settembre, con un massimo di presenza da fine giugno a metà luglio. Il rapporto fra i due sessi (abbastanza vicino a 1) non sembra variare significativamente dei diversi momenti dell'anno.

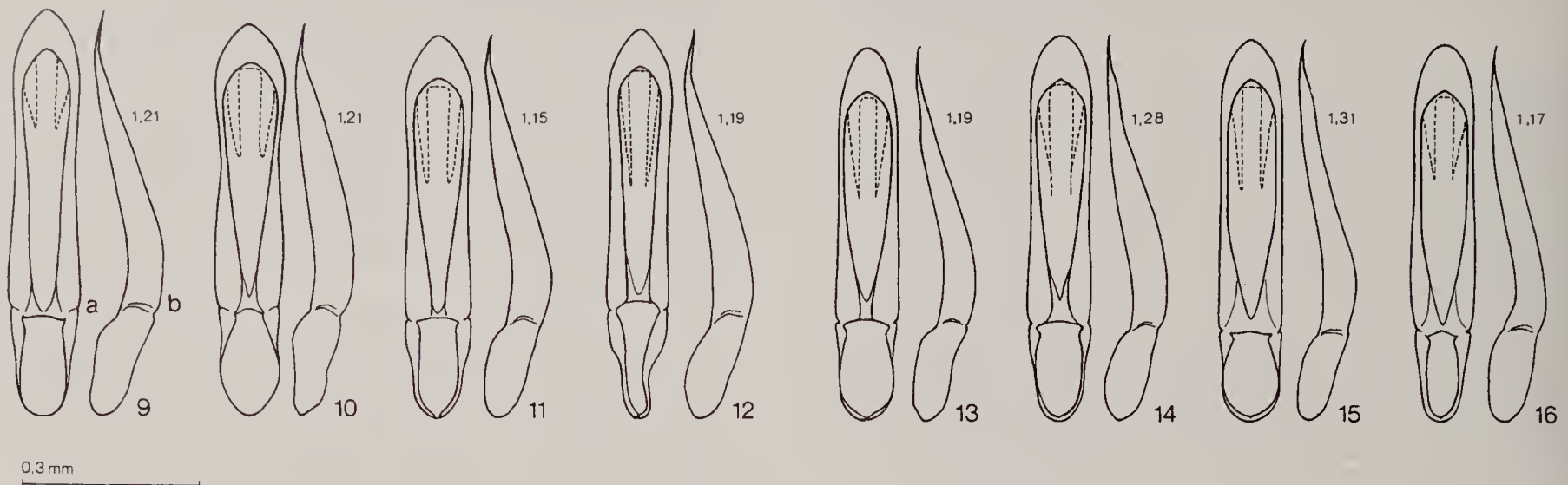
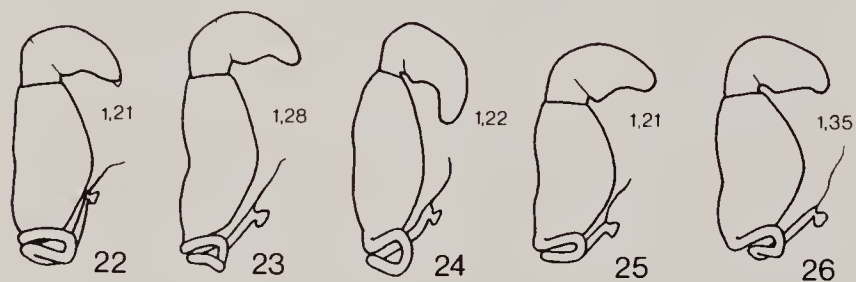
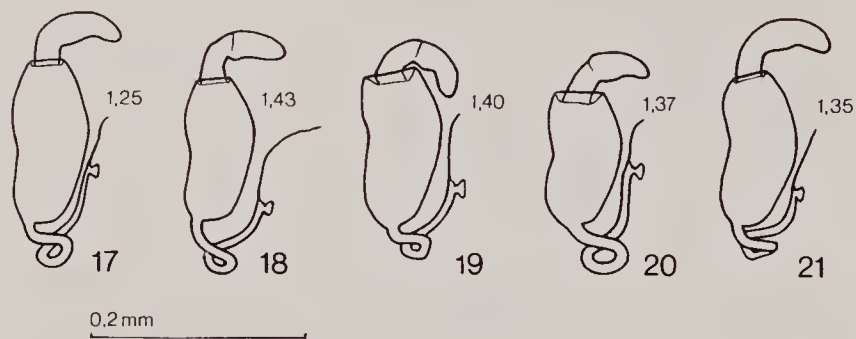
Longitarsus (s. str.) fulgens (Foudras, 1860)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Piemonte.
Piante ospiti: Lamiacee dei generi *Mentha*, *Lycopus* e *Scutellaria*.
Note biologiche: *L. fulgens* è un insetto caratteristico di prati molto umidi. Abbiamo riscontrato la sua presenza solo nella palude di Ca' di Sala, dove peraltro era molto raro.

Longitarsus (s. str.) brunneus (Duftschmid, 1825)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Friuli-Venezia Giulia, Lombardia (prima segnalazione) Piemonte, Liguria, Toscana, Abruzzo, Lazio, Campania, Calabria.
Piante ospiti: Ranuncolacee del genere *Thalictrum*. Secondo Gruev anche Asteracee (*Aster*), Boraginacee (*Symphytum*) e Lamiacee (*Stachys*). Per quanto riguarda il Monte Barro l'insetto è stato raccolto costantemente su *Thalictrum*, prevalentemente *Thalictrum minus*.
Note biologiche: abbiamo raccolto femmine con uova dalla prima decade di maggio alla fine di giugno e un maschio fortemente immaturo a metà luglio; nessun esemplare di *L. brunneus* è stato raccolto in agosto, settembre e ottobre, pur essendo soprattutto questi i mesi in cui, sulla base dell'esperienza acquisita dall'esame di materiale di altra provenienza (Venezia Giulia), dovrebbero comparire individui immaturi. Per quanto riguarda la proporzione fra i due sessi abbiamo rilevato una maggiore presenza di maschi, soprattutto nel mese di maggio

Longitarsus (s. str.) minusculus (Foudras, 1860)
Corotipo: S-Europeo (SEU).
Presenza in Italia: Friuli-Venezia Giulia, Lombardia (prima segnalazione), Piemonte, Liguria, Emilia-Romagna, Toscana, Lazio, Puglia (?).
Piante ospiti: Lamiacee, soprattutto dei generi *Stachys*, *Teucrium*, *Sideritis* e *Salvia*.
Note sistematiche: *L. minusculus* è stato citato anche di Lucania, Sicilia (Biondi, 1990: 145) e Sardegna (Leonardi, 1975: 9; Biondi, 1990: 145) dove invece sembra essere sostituito da *L. anacardius* (All.); quest'ultimo è un taxon a distribuzione sud-mediterranea che è stato messo in sinonimia del *L. minusculus* da Warchalowski (1969); successivamente uno di noi (Leonardi) ebbe modo di esaminare due femmine della serie tipica di *L. anacardius* nella collezione Oberthür e, ritenendo il taxon una specie distinta, designò una di esse come Lectotypus, designazione che è però rimasta in litteris. Doguet nel volume sugli Alticinae della serie Faune de France (1994: 216) rivaluta *L. anacardius*, considerandolo sottospecie di *L. minusculus*; le importanti differenze (soprattutto nella conformazione della spermateca: Figg. 17-26) che permettono di separarlo dal *L. minusculus*, fanno preferire l'ipotesi che esso sia effettivamente una specie a sè stante ([1]). Nel complesso le due entità si possono riconoscere in base ai seguenti caratteri:

1 Microttero. Le/Lp (v. Fig. 27) nei maschi normalmente < 3,20, nelle femmine normalmente < 3,40. lp/Lp (v. Fig. 28) nei maschi normalmente < 1,45, nelle femmine normalmente < 1,50. Edeago in visione ventrale (Figg. 9a-12a) con una leggera strozzatura circa ai 3/5 distali della sua lunghezza e con apice subtriangolare, in visione laterale

(Figg. 9b-12b) caratterizzato quasi sempre da una leggera deflessione apicale. Spermateca (Figg. 22-26) con parte distale molto larga e non invaginata nella parte basale; ansa del ductus appressata al corpo della spermateca. Europa centrale e meridionale ....*L. minusculus* (Foudras)

1' Spesso macrottero. Le/Lp (v. Fig. 27) nei maschi normalmente > 3,40, nelle femmine normalmente > 3,50. lp/Lp (v. Fig. 28) nei maschi normalmente > 1,45, nelle femmine normalmente > 1,50. Edeago in visione ventrale (Figg. 13a-16a) nella metà distale con lati praticamente paralleli e apice di regola arrotondato, in visione laterale (Figg. 13b-16b) con deflessione apicale in genere più debole o del tutto assente. Spermateca (Figg. 17-21) con parte distale più sottile e debolmente invaginata nella parte basale; ansa del ductus più staccata dal corpo della spermateca. Is. Baleari, Sardegna, Sicilia, Lucania, Maghreb..*L. anacardius* (Allard)

Figg. 9-16 - Edeagi di *Longitarsus minusculus* (9-12) e *L. anacardius* (13-16) in visione ventrale (a) e laterale (b). I numeri piccoli indicano la lunghezza elitrale in millimetri degli esemplari disegnati. Località degli esemplari raffigurati: Monte Barro (9-10); Lazio, Riofreddo (11); Bohemia, Karlstein (12); Algeria, Constantine (13); Algeria, El Meridj (14); Tunisia, Le Kef (15); Sardegna, Gennargentu (16).

Figg. 17-26 - Spermateche di *Longitarsus anacardius* (17-21) e *L. minusculus* (22-26) in visione dorsale. I numeri piccoli indicano la lunghezza elitrale in millimetri degli esemplari disegnati. Località degli esemplari raffigurati: Basilicata, Policoro (17); Algeria, Algier («ex Musaeo Allard»): Lectotypus + Paralectotypus (18-19); Algeria, El Meridj (20); Algeria, Bône (21); Istria, Mali Kras (22); Friuli Venezia Giulia, Duino (23); Monte Barro (24); Lazio, Riofreddo (25); Friuli Venezia Giulia, Bivio Aurisina (26).

Longitarsus* (s. str.) *linnaei linnaei (Duftschmid, 1825)

Corotipo: S-Europeo (SEU).

Presenza in Italia: tutte le regioni.

Piante ospiti: Boraginacee, soprattutto del genere *Symphytum*.

Note biologiche: sul Monte Barro è stato raccolto solo nei boschi di latifoglie della Val Faè.

Longitarsus* (s. str.) *pinguis Weise, 1888

Corotipo: S-Europeo (SEU).

Presenza in Italia: Friuli-Venezia Giulia, Veneto, Trentino-Alto Adige, Lombardia, Emilia-Romagna, Abruzzo.

Piante ospiti: Boraginacee. All'interno del Parco del Monte Barro abbiamo raccolto il *L. pinguis* quasi esclusivamente in Val Faè, senza riuscire a individuare con certezza la pianta ospite. L'insetto è invece molto comune nelle vicinanze del Lago d'Alserio, a poca distanza dal Monte Barro, dove è stato raccolto da uno di noi (Leonardi) su *Pulmonaria officinalis*.

Note biologiche: è stata riscontrata la presenza di individui immaturi nel mese di settembre.

Note sistematiche: gli esemplari alpini di *L. pinguis* fanno pensare a forme molto scure di *L. luridus* (Scop.), dalle quali si differenziano per le elitre in genere più largamente arrotondate all'apice (Figg. 29-31) e digradanti sui fianchi in un arco un po' meno re-

([1]) A lavoro ultimato abbiamo ricevuto un articolo di Doguet, Bastazo, Bergeal & Vela in cui si considera *L. anacardius* specie distinta e si fissa come Lectotypus l'esemplare di cui è rappresentata la spermateca nella fig. 18 della nostra pubblicazione.

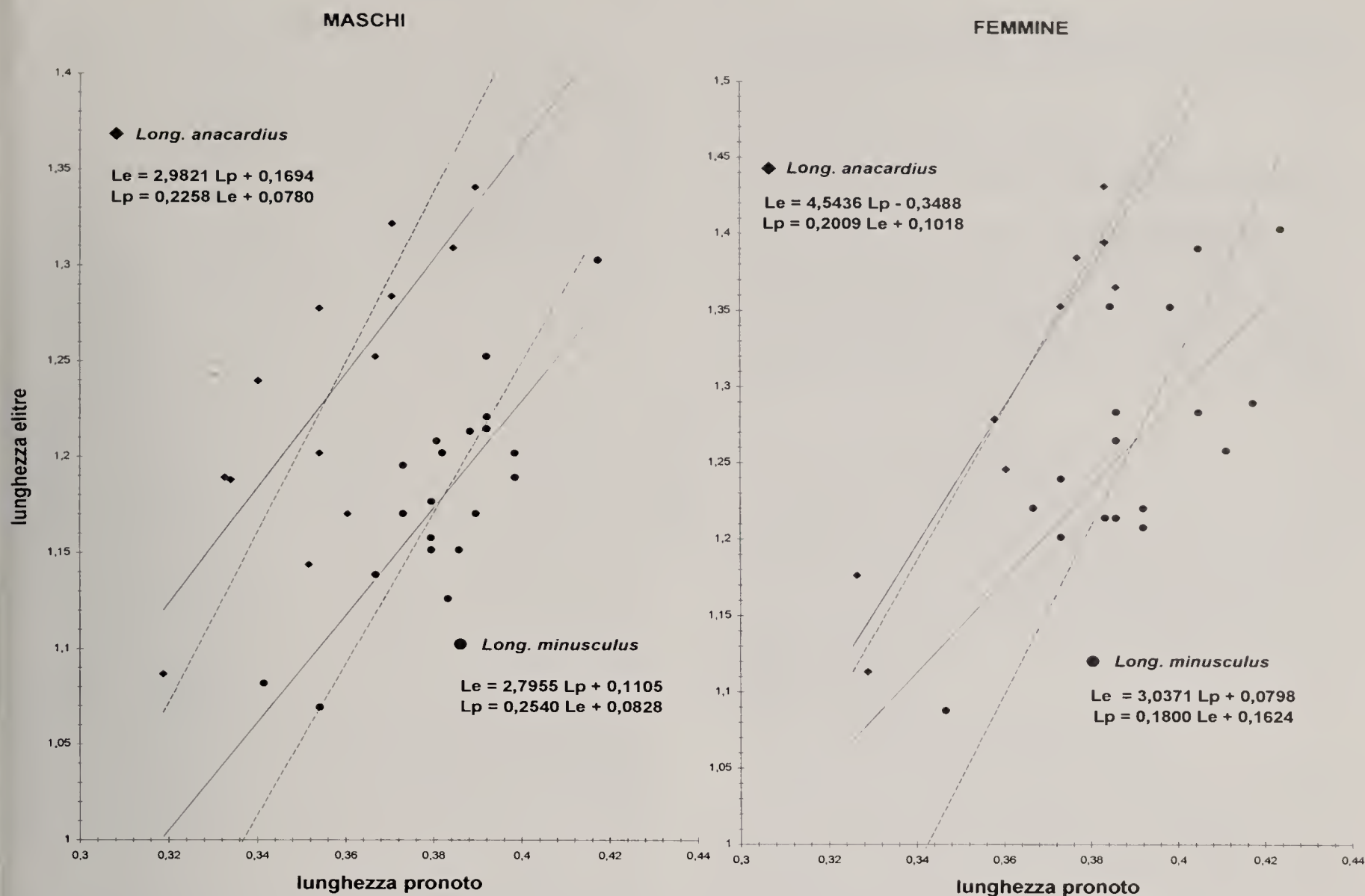



Fig. 27 - Variabilità della lunghezza delle elitre e del pronoto in *Longitarsus anacardius* e *L. minusculus* (valori in millimetri). Le rette che descrivono la regressione di Le su Lp sono tracciate con una linea continua, quelle che descrivono la regressione di Lp su Le sono tracciate con una linea tratteggiata. L'analisi della covarianza applicata alle rette ha fornito i seguenti risultati: maschi: F= 93,57 (Lp su Le, differenza altamente significativa); F= 64,53 (Le su Lp, differenza altamente significativa); femmine: F= 47,44 (Lp su Le, differenza altamente significativa); F= 30,23 (Le su Lp, differenza altamente significativa).

golare. Nella regione appenninica la forma elitrale presenta una variabilità più marcata (Figg. 32-41) e possono comparire individui con elitre accentuatamente compresse ai lati e debolmente subtroncate, che fanno pensare piuttosto a *L. anchusae* (Paykull) o a *L. bonnairei* (Allard). Altrettanto variabili sono il rapporto lp/Lp, i cui valori medi comunque non sembrano essere mai inferiori a 1,30, e la conformazione dell'organo copulatore (Figg. 44-50): nell'edeago degli esemplari appenninici in genere il lembo interno del bordo laterale è fortemente inclinato verso il fondo della scanalatura ventrale, cosicchè il bordo appare più stretto e la scanalatura più larga, inoltre l'apice è in visione ventrale abitualmente meno ottuso che nella forma alpina e in visione laterale mediamente meno deflesso; gli esemplari quasi privi di deflessione edeagica apicale (Figg. 46-47) ricordano, per questa caratteristica, *L. bulgaricus* Gruev.

Esemplari abbastanza simili a quelli europei sono stati raccolti nella regione caucasica, mentre in Israele è diffusa una forma con protorace relativamente poco trasverso (lp/Lp abitualmente < 1,25) e margine apicale delle elitre costantemente subtroncato (Figg. 42-43) che, pur essendo di chiara derivazione dal *L. pinguis*, col quale ha in comune sia la conformazione dell'edeago (Fig. 51) che quella della spermateca, è stata trattata da Furth (1979: 116) come specie distinta col nome di *L. truncatellus* Weise.

Per la relativa brevità della callosità elitropleurale, che si ferma all'inizio del margine apicale delle elitre, e per la presenza di individui con elitre fortemente compresse e subtroncate *L. pinguis* dovrebbe essere incluso nel sottogenere *Testergus* Wse sensu Bechyné (= *Truncatus* Pal.), ipotesi, questa, non sconvolgente, dato che Heikertinger lo trattava addirittura come varietà di *L. anchusae*, cioè di una specie che Lopatin (1977) include in questo sottogenere. D'altro canto, la prima di queste caratteristiche può comparire, con maggiore o minore frequenza, anche in alcuni *Longitarsus* attribuiti al sottogenere tipico, quali, per esempio, *L. reichei* (All.), *L. medvedevi* Shap., *L. albineus* (Foudr.), e *L. absynthii* Kutsch., mentre le altre, data la loro variabilità, fanno di *L. pinguis*, una specie di transizione fra *Longitarsus* s. str. e *Testergus* Weise sensu Bechyné. Riteniamo pertanto che quest'ultimo (che Bechyné proponeva addirittura come genere distinto) sia troppo insufficientemente caratterizzato dal punto di vista morfologico per poter essere considerato come un sottogenere distinto, pur essendo probabile che molti dei taxa che vi sono inclusi formino realmente un gruppo naturale. È questa la posizione sostenuta dalla maggior parte degli specialisti (v. Doguet, 1994). Una sua eventuale rivalutazione potrà essere, a nostro avviso, solo successiva a uno studio filogenetico accurato dell'intero genere *Longitarsus*.

Non intendiamo invece entrare nel merito della validità del sottogenere *Testergus* inteso nel senso originale, che Weise istituì per due specie caucasiche

MASCHI

◆ Long. anacardius

lp = 1,0955 Lp + 0,1374
Lp = 0,7473 lp - 0,0381

● Long. minusculus

lp = 1,0582 Lp + 0,1371
Lp = 0,6479 lp + 0,0314

larghezza pronoto

lunghezza pronoto

FEMMINE

◆ Long. anacardius

lp = 1,3519 Lp + 0,0660
Lp = 0,7020 lp - 0,0278

● Long. minusculus

lp = 1,3045 Lp + 0,0561
Lp = 0,4962 lp + 0,1098

larghezza pronoto

lunghezza pronoto

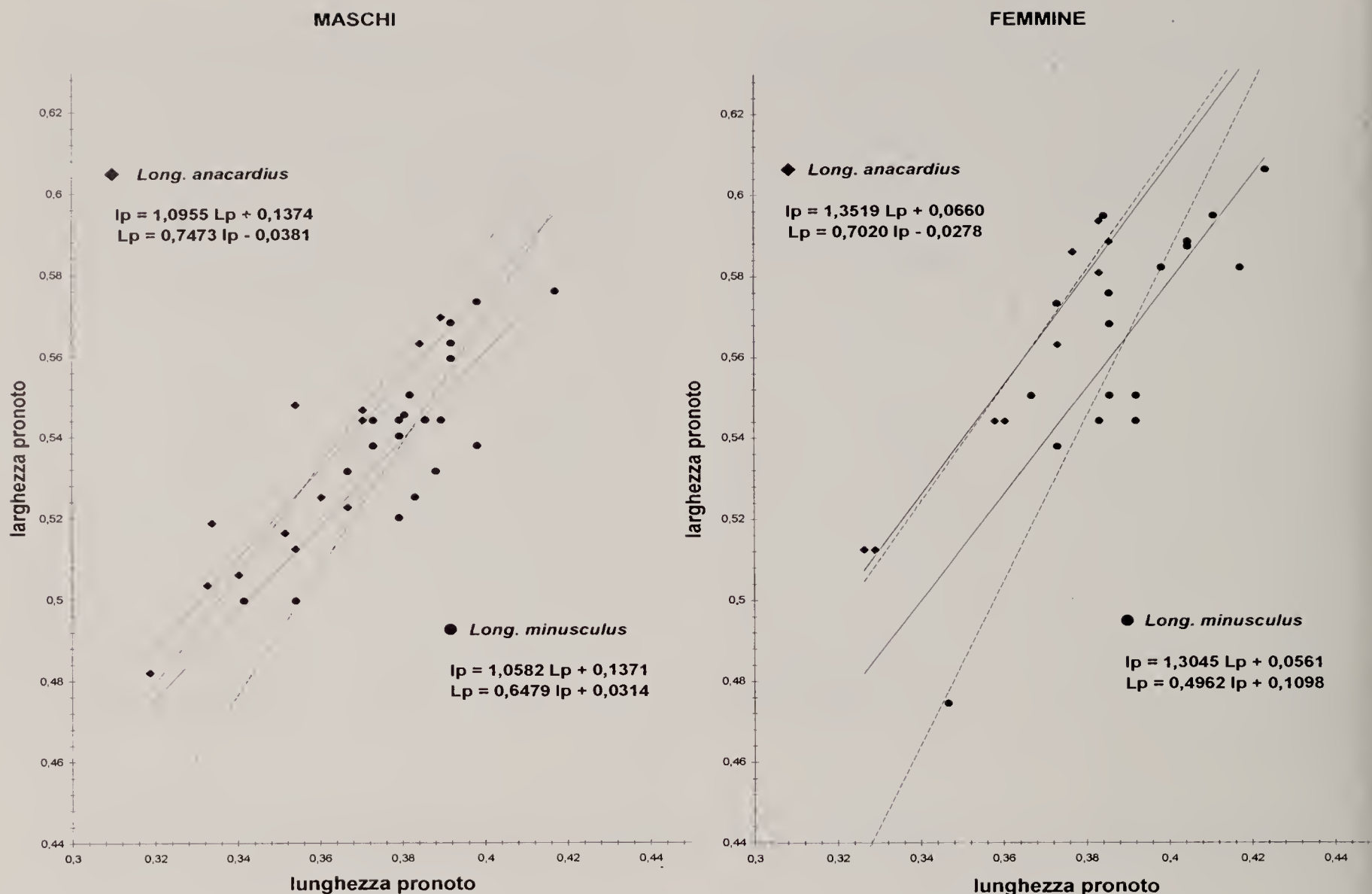
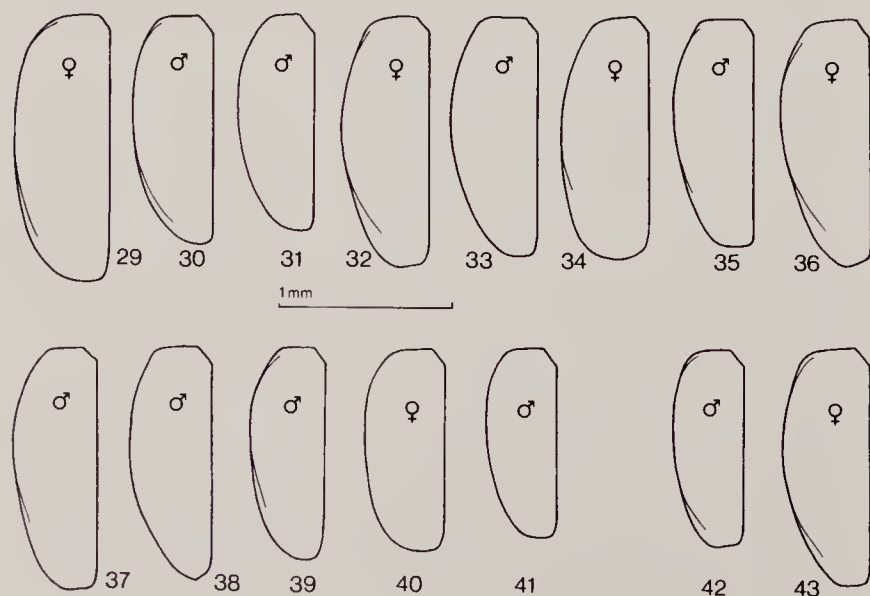



Fig. 28 - Variabilità delle dimensioni del pronoto in *Longitarsus anacardius* e *L. minusculus* (valori in millimetri). Le rette che descrivono la regressione di lp su Lp sono tracciate con una linea continua, quelle che descrivono la regressione di Lp su lp sono tracciate con una linea tratteggiata. L'analisi della covarianza applicata alle rette ha fornito i seguenti risultati: maschi: F= 7,57 (lp su Lp, differenza significativa); F= 22,51 (Lp su lp, differenza altamente significativa); femmine: F= 12,54 (lp su Lp, differenza altamente significativa); F= 25,97 (Lp su lp, differenza altamente significativa).

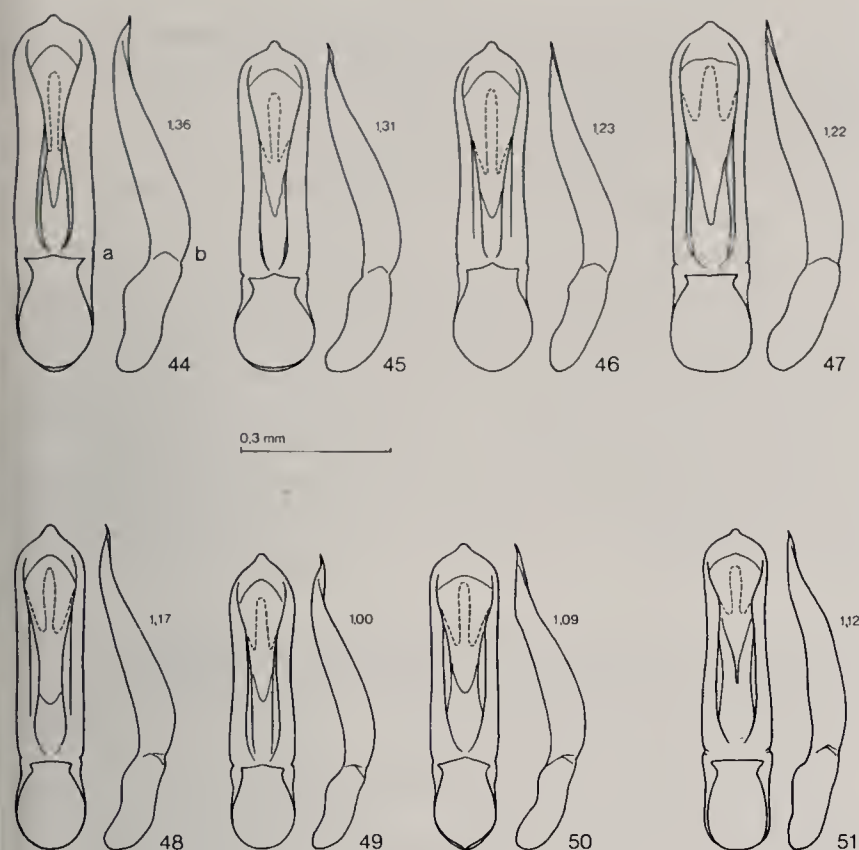
(*L. lederi* e *L. pubescens*) da lui stesso descritte, caratterizzate dalle elitre saldate e pubescenti.

Altica oleracea (Linneo, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Piante ospiti: soprattutto poligonacee ma anche

Figg. 29-43 - Silouette elitrale in *Longitarsus pinguis* (29-41) e *L. truncatellus* (42-43). Località degli esemplari raffigurati: Monte Barro (20-30); Nieder Bayern (31); Emilia Romagna, Campigna (32-34); Emilia Romagna, Passo Calla (35); Campania, Valle Piana (M.ti Picentini) (36); Abruzzo, Monte Marsicano (37); Molise, Monte Miletto (38); Abruzzo, Gran Sasso (39); Abruzzo, Blockhaus (40-41); Israele, N. Amud (42-43).

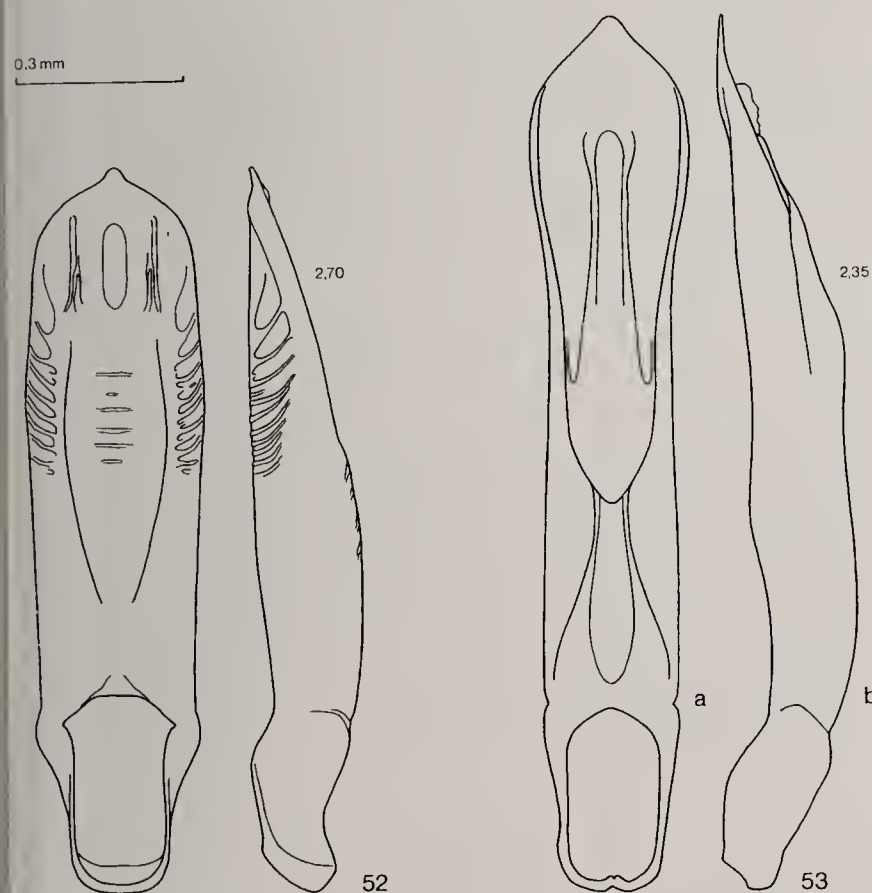
Ericacee, Onagracee, Litracee, Cistacee, Rosacee, Scrofulariacee, Betulacee, Fagacee.

Altica carinthiaca (Weise, 1888), (Fig. 52)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: Alpi (finora citata in modo generico delle Alpi Orientali e, dubitativamente, delle Alpi Marittime; la presenza di questa specie sul Monte Barro costituisce il primo dato sicuro per le Alpi Italiane), Lazio.
Piante ospiti: come piante ospiti di *A. carinthiaca* figurano *Sanguisorba minor* (Rosacee) e *Lathyrus pratensis* (Fabacee); data la rarità di questa specie non siamo riusciti a confermare questi dati biologici

Altica impressicollis Reiche, 1862
Corotipo: Turanico-Europeo-Mediterraneo (TEM)
Presenza in Italia: tutte le regioni.
Piante ospiti: Enoteracee del genere *Epilobium*, Litracee (*Lythrum salicaria*), Asteracee (*Eupatorium cannabinum*.
Note biologiche: Euforbiacee del genere *Mercurialis.* Questa specie frequenta biotopi umidi. L'abbiamo raccolta, in un numero limitato di esemplari, solo nella palude di Ca' di Sala.

Hermaeophaga mercurialis (Fabricius, 1792)
Corotipo: Europeo (EUR)
Presenza in Italia: regioni settentrionali, Lazio, Abruzzo, Puglia.

Figg. 44-51 - Edeagi di *Longitarsus pinguis* (44-50) e *L. truncatellus* (51) in visione ventrale (a) e laterale (b). I numeri piccoli indicano la lunghezza elitrale in millimetri degli esemplari disegnati. Località degli esemplari raffigurati: Görz Plava (44); Monte Barro (45); Liguria, Rezzoaglio d'Aveto (46); Emilia Romagna, Campigna (47); Abruzzo, Monte Marsicano (48); Abruzzo, Blockhaus (49-50); Israele (51).

Piante ospiti: Euforbiacee del genere *Mercurialis*. Questo insetto è stato raccolto solo in Val di Faè, dove è frequente soprattutto nel sottobosco.

Lythraria salicariae (Paykull, 1800)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e centrali, Campania, Basilicata, Calabria.
Piante ospiti: Primulacee del genere *Lysimachia*, Litracee (*Lythrum salicaria*).

Figg. 52-53 - Edeagi di *Altica carinthiaca* (52) e *Asiorestia crassicornis* (53) del Monte Barro in visione ventrale (a) e laterale (b). I numeri piccoli indicano la lunghezza elitrale in millimetri degli esemplari disegnati.

Note biologiche: questa specie è caratteristica di biotopi umidi; l'abbiamo raccolta solo nella palude di Ca' di Sala.

Asiorestia brevicollis (J. Daniel, 1904)
Corotipo: Sud-Europeo (SEU) (endemita Alpino-Appenninico).
Presenza in Italia: tutte le regioni peninsulari ad esclusione di Valle d'Aosta, Piemonte e Liguria.
Piante ospiti: Asteracee del genere *Cirsium*.
Note biologiche: questo insetto sembra prediligere ambienti umidi; ne abbiamo raccolto una sola femmina nella palude di Ca' di Sala, ed era già noto del Lago di Annone.

Asiorestia transversa (Marsham, 1802)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni peninsulari e Sardegna.
Piante ospiti: Asteracee soprattutto del genere *Cirsium*, Boraginacee (?), Plumbaginacee (?).
Note biologiche: il rapporto maschi/femmine ha fornito il valore 0,79 in un campione di 41 esemplari raccolto il 15.6.1990.

Asiorestia ferruginea (Scopoli, 1763)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni.
Piante ospiti: Poacee, Fabacee, Poligonacee, Asteracee, Boraginacee, Cannabacee, Urticacee.

Asiorestia crassicornis crassicornis (Faldermann, 1837), (Fig. 53)
Corotipo: S-Europeo (SEU).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Lombardia (prima segnalazione per la regione), Valle d'Aosta, Liguria, Emilia-Romagna (M. Fumaiolo, dato inedito).
Piante ospiti: Asteracee del genere *Centaurea*.

Orestia electra electra Gredler, 1868
Corotipo: S-Europeo (SEU) (endemita Alpino)
Presenza in Italia: ssp. *electra*: Trentino-Alto Adige (Alpi Giudicarie), Lombardia; ssp. *brunnea* (Halbherr, 1898): Trentino-Alto Adige, Veneto.
Note biologiche: questa specie non frequenta la vegetazione; la si raccoglie sotto sassi, fra i muschi o nelle lettiere. Sul Monte Barro ne è stato raccolto un solo maschio in Val Faè a m 620 di quota.

Derocrepis sodalis (Kutschera, 1860)
Corotipo: S-Europeo (SEU) (endemita Alpino-Appenninico).
Presenza in Italia: regione alpina (dalle Alpi Retiche alle Liguri), Appennino centro-settentrionale, Massiccio del Pollino.
Piante ospiti: Fabacee.

Crepidodera aurea (Geoffroy, 1785)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e centrali, Campania, Basilicata, Calabria, Sicilia.
Piante ospiti: Salicacee.

Crepidodera aurata (Marsham, 1802)
Corotipo: Asiatico-Europeo (ASE)
Presenza in Italia: tutte le regioni.
Piante ospiti: Salicacee.
Note sistematiche: di questa specie Heikertinger

(1910: (54)) ha descritto, su esemplari di Morea, la razza *peloponnesiaca*. Noi abbiamo potuto esaminare una serie di esemplari (MM, CZ) raccolti in Peloponneso (Korinthia: dint. Kaliani, 13.IX.1995) da S. Zoia, che corrispondono alla descrizione di questo taxon; essi non appartengono sicuramente alla specie *aurata*, dalla quale si distinguono, oltre che per la conformazione dell'edeago e della spermateca, anche per caratteristiche esterne, quali, soprattutto, la relativa opacità elitrale. Riteniamo quindi che *Crepidodera peloponnesiaca* sia una specie distinta o, forse, una forma geografica di *Cr. nigricoxis* All., che conosciamo solo dalle descrizioni (Gruev & Tomov, 1986: 273, 274; Konstantinov, 1996: 29, 31-32). A favore della seconda ipotesi sembra giocare una notevole rassomiglianza, sia edeagica che spermatecale, fra i due taxa; in nessuna descrizione di *Cr. nigricoxis* si accenna però alla scarsa lucentezza elitrale, che caratterizza invece *Cr. peloponnesiaca*.

Epitrix pubescens (Koch, 1803)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: regioni settentrionali e centrali, Basilicata, Sardegna.
Piante ospiti: Solanacee.

Podagrica fuscicornis (Linneo, 1766)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Piante ospiti: Malvacee, occasionalmente Asteracee del genere *Carduus*.
Note sistematiche: per la punteggiatura elitrale relativamente forte gli esemplari del Monte Barro sembrano appartenere alla forma mediterranea, abitualmente trattata come sottospecie, col nome di *chrysomelina* (Waltl, 1835); il valore di questa razza geografica può essere facilmente messo in discussione in considerazione dell'elevata variabilità della specie e dell'esistenza di troppe popolazioni con caratteristiche intermedie.

Mantura (s. str.) obtusata (Gyllenhal, 1813)
Corotipo: Europeo (EUR).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Lombardia, Piemonte, Emilia-Romagna, Toscana, Lazio, Campania, Calabria, Sicilia.
Piante ospiti: Poligonacee del genere *Rumex*.

Chaetocnena (Tlanoma) concinna (Marsham, 1802)
Corotipo: Asiatico-Europeo (ASE)
Presenza in Italia: regioni peninsulari, Sicilia, Sardegna (?).
Piante ospiti: Poligonacee dei generi *Polygonum* e *Rumex*, Chenopodiacee del genere *Atriplex*.

Chaetocnema (Tlanoma) laevicollis (C. G. Thomson, 1866)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Friuli-Venezia Giulia, , Veneto, Lombardia, Piemonte, Lazio.
Piante ospiti: Poligonacee, occasionalmente Brassicacee.

Chaetocnema (Tlanoma) tibialis (Illiger, 1807)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Piante ospiti: Chenopodiacee.

Chaetocnema (Tlanoma) conducta (Motschulski, 1838)
Corotipo: Turanico-Europeo-Mediterraneo (TEM), secondariamente Afrotropicale.
Presenza in Italia: tutte le regioni.
Piante ospiti: Ciperacee, Giuncacee, Poacee.

Chaetocnema (s. str.) confusa (Bohemann, 1851)
Corotipo: Turanico-Europeo (TUE)
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Piemonte, Campania, Basilicata, Calabria.
Piante ospiti: Ciperacee del genere *Carex*, Giuncacee del genere *Juncus*.
Note biologiche: si tratta di un insetto tipico di ambienti umidi: l'abbiamo raccolto solo nella palude di Ca' di Sala.

Chaetocnema (s. str.) arida Foudras, 1860
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: regioni settentrionali e centrali, Basilicata, Sicilia, Sardegna.
Piante ospiti: Ciperacee, Giuncacee.

Chaetocnema (s. str.) hortensis (Geoffroy, 1785)
Corotipo: Paleartico (PAL), secondariamente Afrotropicale.
Presenza in Italia: tutte le regioni.
Piante ospiti: Poacee, Ciperacee (?).

Sphaeroderma testaceum (Fabricius, 1775)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni peninsulari, Sicilia.
Piante ospiti: Asteracee dei generi *Carduus* e *Cirsium*.

Sphaeroderma rubidum (Graëlls, 1858)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutte le regioni.
Piante ospiti: Asteracee soprattutto dei generi *Centaurea*, *Carduus* e *Cirsium*.

Argopus ahrensi (Germar, 1817)
Corotipo: S-Europeo (SEU).
Presenza in Italia: regioni nordorientali, Lombardia, Piemonte, Toscana, Abruzzo, Calabria.
Piante ospiti: Ranuncolacee del genere *Clematis*.

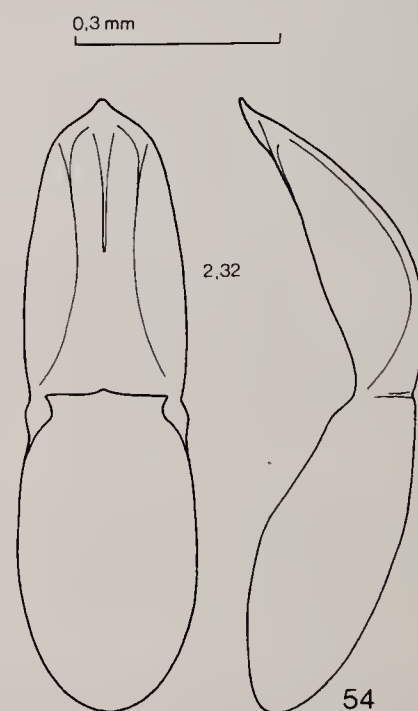



Fig. 54 - Edeago di *Dibolia foersteri* del Monte Barro in visione ventrale (a) e laterale (b). Il numero piccolo indica la lunghezza elitrale in millimetri dell'esemplare disegnato.

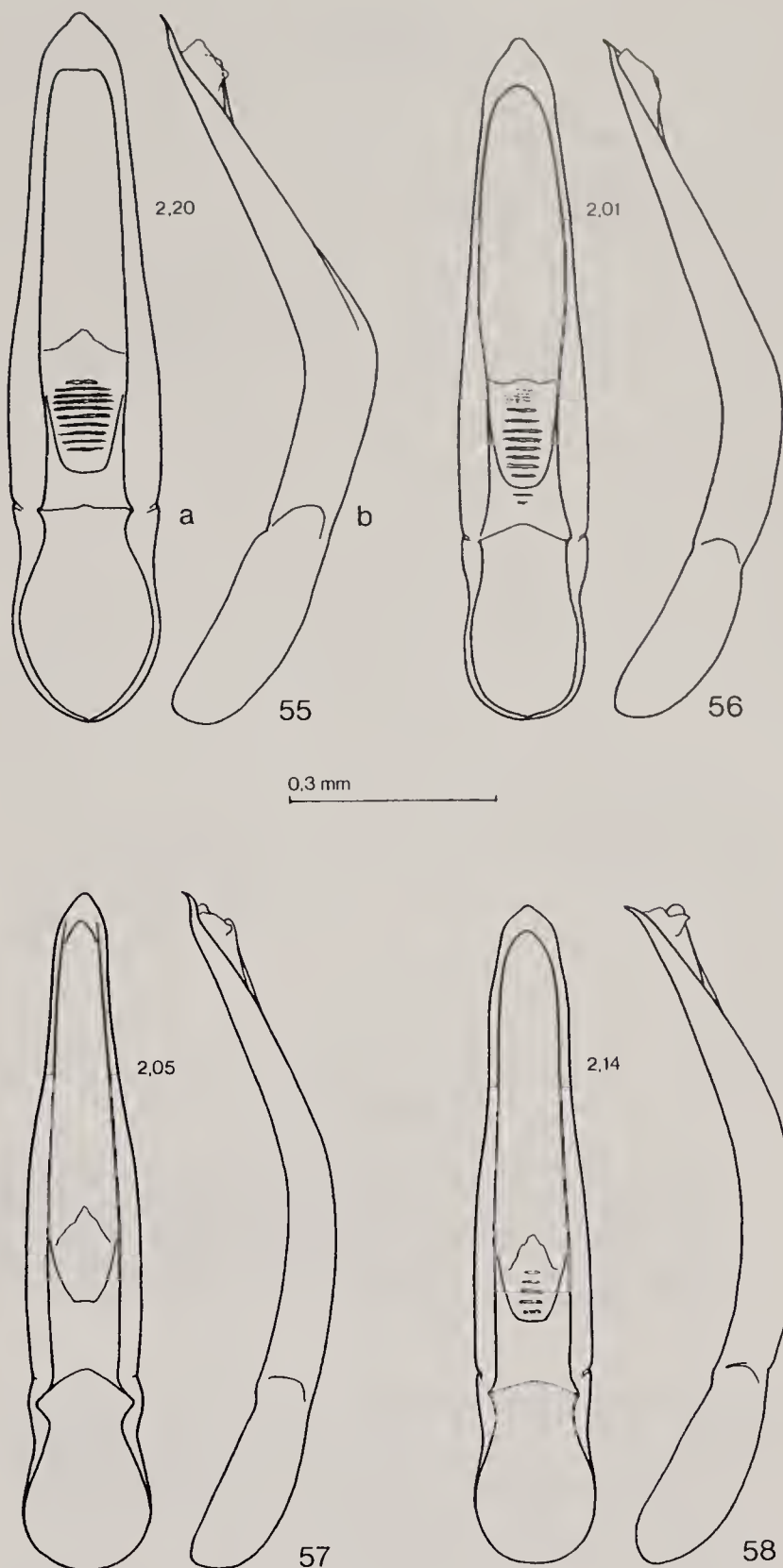
Dibolia foersteri Bach, 1859, (Fig. 54)
Corotipo: Europeo (EUR).
Presenza in Italia: Friuli-Venezia Giulia, Veneto, Trentino-Alto Adige, Lombardia (prima segnalazione per questa regione), Piemonte, Lazio.
Piante ospiti: Lamiacee (*Stachys officinalis*).

Dibolia cryptocephala (Koch, 1803)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: regioni settentrionali, Toscana, Abruzzo, Basilicata, Calabria, Sicilia.
Piante ospiti: Lamiacee, probabilmente dei generi *Thymus* e *Salvia*. *Salvia pratensis* è presente sul Monte Barro in tutte e tre le stazioni in cui abbiamo raccolto questo insetto.

Psylliodes affinis (Paykull, 1799)
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM)
Presenza in Italia: regioni settentrionali e centrali, Campania, Basilicata, Sardegna.
Piante ospiti: Solanacee, soprattutto *Solanum dulcamara*.

Psylliodes napi (Fabricius, 1792)
Corotipo: Turanico-Europeo-Mediterraneo (TEM).
Presenza in Italia: tutte le regioni.
Piante ospiti: Brassicacee.

Psylliodes toelgi Heikertinger, 1914
Corotipo: S-Europeo (SEU).
Presenza in Italia: Friuli-Venezia Giulia, Trentino-Alto Adige, Lombardia, Piemonte, Val d'Aosta, Lazio (Terminillo: Sella di Leonessa, dato inedito).
Piante ospiti: Brassicacee (*Biscutella laevigata*).
Note biologiche: individui immaturi sono stati raccolti nei mesi di giugno e di luglio.
Note sistematiche: *Ps. toelgi* è una specie montana molto vicina a *Ps. brisouti* Bedel; se ne distingue soprattutto per il primo protarsomero dei maschi modestamente dilatato, per l'assenza del tipo alare brachittero (nella popolazione del Monte Barro domina la forma mesottera con una percentuale di circa il 15% di individui macrotteri) e per l'edeago (Figg. 57-58) mediamente più esile e meno angolosamente arcuato; ulteriori particolarità edeagiche si riscontrano nella scanalatura ventrale, dove la parte basale è relativamente lunga e la rigatura trasversale della parte intermedia è spesso molto debole o del tutto assente. Il confronto (Figg. 59-60) fra i valori di Le, Lp, Lt ed Ld ottenuti da un campione di *Ps. toelgi* del Monte Barro e quelli ottenuti da un campione di *Ps. brisouti* della stessa provenienza conferma inoltre l'esistenza di importanti differenze nei valori medi del rapporto Le/Lp ed Lt/Ld, in sostanziale accordo con quanto fu già scritto da uno di noi (Leonardi, 1971). È da notare come gli individui del Monte Barro, forse in relazione alla quota molto bassa (circa 300 m) del ritrovamento, presentino dimensioni medie notevolmente superiori rispetto ai valori medi della specie.

Psylliodes brisouti Bedel, 1898
Corotipo: S-Europeo (SEU).
Presenza in Italia: Veneto, Lombardia (prima segnalazione per questa regione), Piemonte, Val d'Aosta, Lazio, Abruzzo, Sicilia.
Piante ospiti: Brassicacee del genere *Erysimum*.

Figg. 55-58 - Edeagi di *Psylliodes brisouti* (55-56) e *Ps. toelgi* (57-58) del Monte Barro in visione ventrale (a) e laterale (b). I numeri piccoli indicano la lunghezza elitrale in millimetri degli esemplari disegnati.

Note biologiche: sono stati raccolti diversi individui immaturi nella seconda metà di giugno e all'inizio di luglio.

Note sistematiche: è interessante osservare come il Monte Barro sia l'unica località finora nota in cui sono presenti sia *Ps. brisouti* Bedel che *Ps. toelgi* Heikertinger, a conferma del valore specifico di questi due taxa che presentano indubbiamente un livello di affinità assai elevato. Mentre *Ps. toelgi* vive esclusivamente su *Biscutella laevigata*, *P. brisouti* è stata raccolta solo su *Erysimum virgatum*, ai margini della stazione 2; tutti gli esemplari sono risultati brachitteri e i maschi presentano una forte dilatazione del primo articolo protarsale oltre che un edeago (Figg. 55-56) relativamente robusto e quasi angolosamente arcuato; la scanalatura edeagica ventrale presenta spesso un'evidente rigatura trasversale, che tipicamente interessa la parte intermedia ma talvolta si estende an-

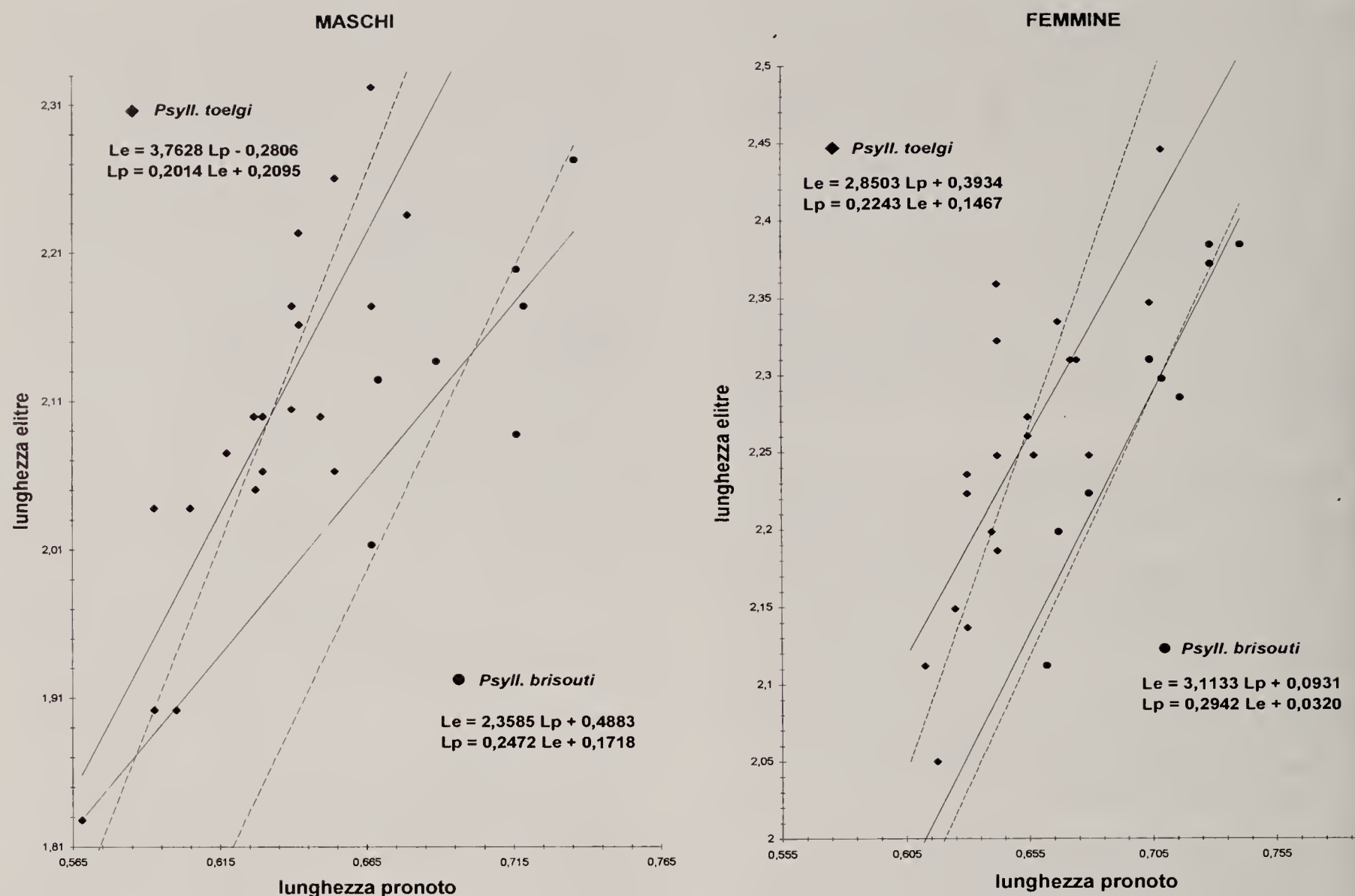



Fig. 59 - Variabilità della lunghezza delle elitre e del pronoto in esemplari di *Psylliodes brisouti* e *Ps. toelgi* del Monte Barro (valori in millimetri). Le rette che descrivono la regressione di Le su Lp sono tracciate con una linea continua, quelle che descrivono la regressione di Lp su Le sono tracciate con una linea tratteggiata. L'analisi della covarianza applicata alle rette ha fornito i seguenti risultati: maschi: F= 78,71 (Lp su Le, differenza altamente significativa); F= 21,99 (Le su Lp, differenza altamente significativa); femmine: F= 54,83 (Lp su Le, differenza altamente significativa); F= 18,41 (Le su Lp, differenza altamente significativa).

che sulla parte basale; quest'ultima, non sempre ben delimitata, è in genere più corta che in *Ps. toelgi*. I valori di Le, Lp, Lt ed Ld, messi a confronto con quelli ottenuti da un campione di *Ps. toelgi* del Monte Barro, sono riportati nelle Figg. 59-60.

Note geometriche: *Ps. brisouti* è nel complesso una specie a gravitazione meridionale, per quanto possa spingersi molto a nord, fino a raggiungere la punta meridionale della Svezia (Baranowski, 1980). 1 Maschio e 1 femmina svedesi conservati presso il Museo di Storia Naturale di Milano (dono Baranowski) forniscono i seguenti dati morfometrici: maschio: Le = 1,840 mm, Lp = 0,605 mm, Lt = 0,740 mm, Ld = 0,177 mm; femmina: Le = 1,950 mm, Lp = 0,640 mm, Lt = 0,778 mm, Ld = 0,177 mm.

Psylliodes cupreus (Koch, 1803)
Corotipo: Centroasiatico-Europeo-Mediterraneo (CEM)
Presenza in Italia: tutte le regioni.
Piante ospiti: Brassicacee.

Psylliodes instabilis Foudras, 1860
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: regioni peninsulari, Sicilia.
Piante ospiti: Brassicacee.

Psylliodes dulcamarae (Koch, 1803)
Corotipo: Turanico-Europeo (TUE)
Presenza in Italia: regioni settentrionali e centrali, Campania, Basilicata, Calabria.
Piante ospiti: Solanacee (*Solanum dulcamara*).

Cassida (Hypocassida) subferruginea Schrank, 1776
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Piante ospiti: Convolvulacee (*Convolvulus*); sporadicamente Chenopodiacee (*Beta*). Un esemplare fu raccolto in Monte Barro su *Calystegia sepium*.

Cassida (Odontionycha) viridis viridis Linnaeus, 1758
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Piante ospiti: specie igro-mesofila, legata a Lamiacee dei generi *Stachys*, *Mentha*, *Galeopsis*, *Lycopus*, *Salvia*. In Monte Barro fu sempre raccolta su *Salvia glutinosa*.

Cassida (s. str.) vibex Linnaeus, 1767
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutte le regioni.
Piante ospiti: Asteracee (*Cirsium*, *Carduus*, *Centaurea*, *Arctium*, *Tanacetum*, *Achillea*). In Monte Barro sembra prevalentemente legata a *Centaurea triumfettii*.

Cassida (s. str.) ferruginea Goeze, 1777
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: penisola.

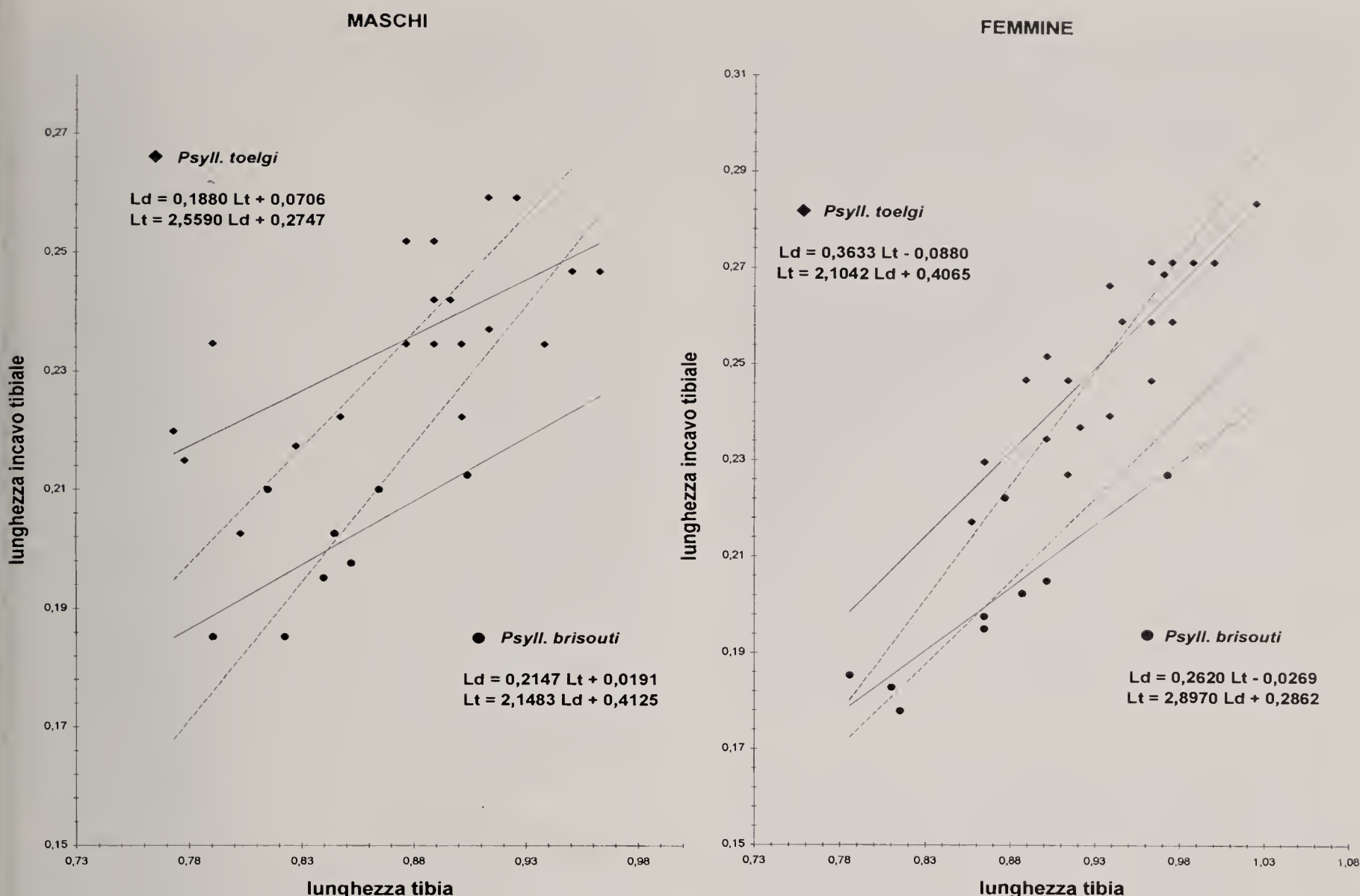



Fig. 60 - Variabilità della lunghezza delle tibie e dell'incavo tibiale in esemplari di *Psylliodes brisouti* e *Ps. toelgi* del Monte Barro (valori in millimetri). Le rette che descrivono la regressione di Ld su Lt sono tracciate con una linea continua, quelle che descrivono la regressione di Lt su Ld sono tracciate con una linea tratteggiata. L'analisi della covarianza applicata alle rette ha fornito i seguenti risultati: maschi: F= 39,39 (Ld su Lt, differenza altamente significativa); F= 4,76 (Lt su Ld, differenza significativa); femmine: F= 40,64 (Ld su Lt, differenza altamente significativa); F= 7,83 (Lt su Ld, differenza significativa).

Piante ospiti: *Pulicaria dysenterica*, su cui fu raccolta anche in Monte Barro.
Note: specie tendenzialmente igrofila.

Cassida (s. str.) rubiginosa rubiginosa Müller, 1776
Corotipo: Paleartico (PAL).
Presenza in Italia: tutte le regioni.
Piante ospiti: diversi generi di Asteracee.

Cassida (s. str.) denticollis Suffrian, 1844
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta la penisola, nel complesso piuttosto rara. Tendenzialmente submontana-montana, specialmente al sud.
Piante ospiti: Asteracee (*Achillea*, *Tanacetum*).

Cassida (s. str.) sanguinolenta sanguinolenta Müller, 1776
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: penisola, Sicilia.
Piante ospiti: Asteracee (*Achillea*, *Tanacetum*).
Note: raccolte femmine con uova a metà luglio.

Cassida (Mionycha) margaritacea Schaller, 1783
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: penisola, Sicilia.
Piante ospiti: Cariofillacee (*Silene*, *Saponaria*, *Spergula*), Lamiacee (*Thymus*), Asteracee (*Centaurea*).
Note: specie tendenzialmente xerofila.

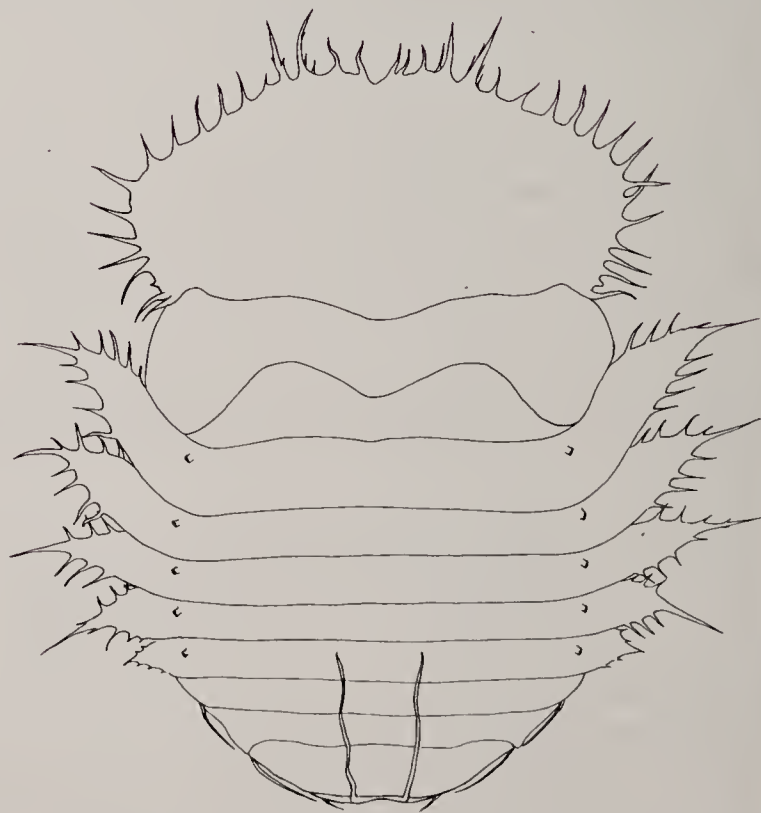
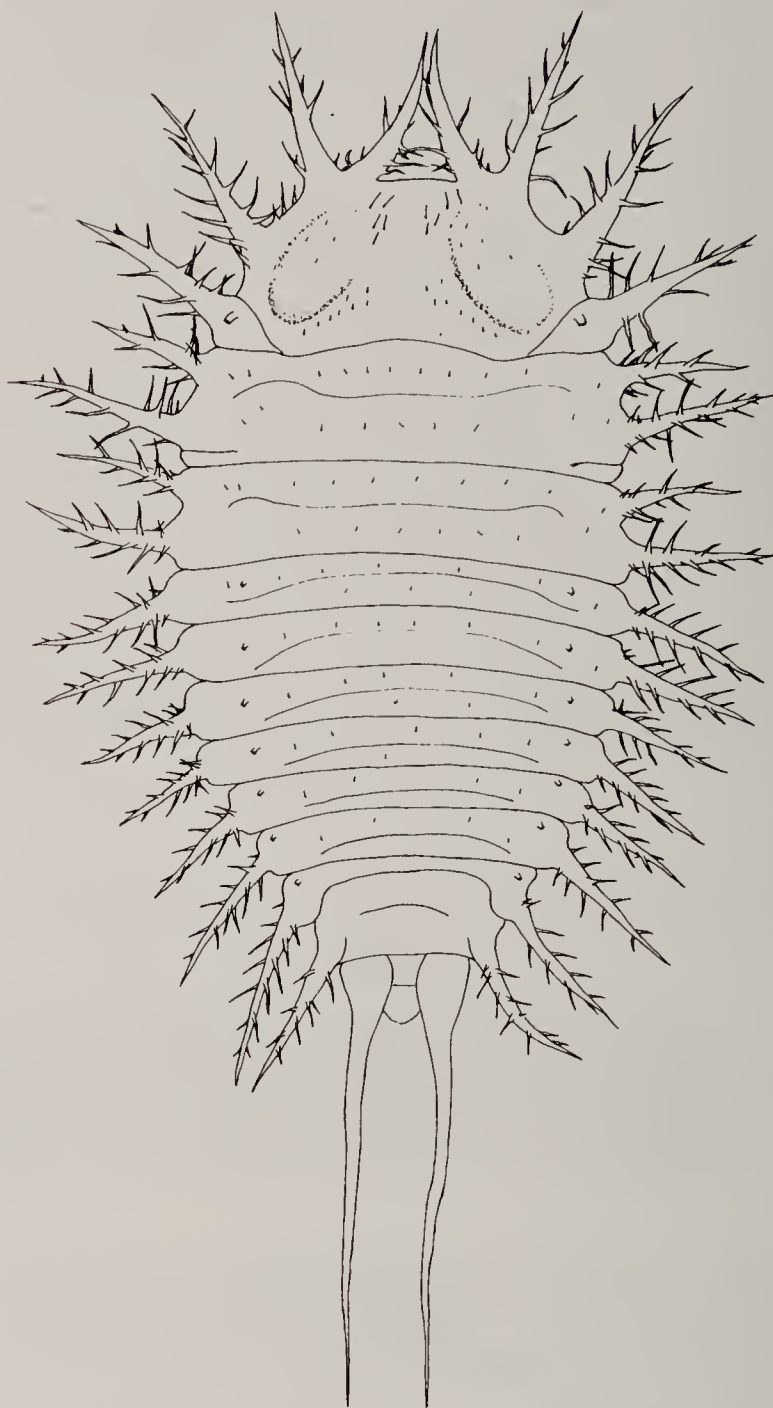
Cassida (Mionycha) subreticulata Suffrian, 1844 (Fig. 66)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: penisola, Sicilia.
Piante ospiti: Cariofillacee (*Silene*, *Saponaria*, *Dianthus*). In Monte Barro raccolta su *Saponaria officinalis*.

Note biologiche: nel corso delle ricerche (16.5.1991) furono raccolti sei esemplari di *Cassida subreticulata* ed allevati con foglie fresche di *Saponaria officinalis*. Gli esemplari cominciarono subito a nutrirsi e ad accoppiarsi frequentemente. Gli accoppiamenti continuarono, con lo stesso ritmo, almeno fino all'inizio di luglio. Il giorno stesso della raccolta iniziarono le prime deposizioni. Dopo breve tempo (22 maggio) erano già state deposte circa 50 uova, contenute singolarmente in piccole ooteche traslucide, formate da un sottile strato di secreto colleterico ricoprente ciascun germe. Nella maggior parte dei casi le ooteche vennero applicate alla pagina superiore delle foglie. La femmina non provvide mai a rivestirle con materiale fecale. Le dimensioni medie delle uova erano 1,15 mm X 0,58 mm. Quelle della intera ooteca 1,58 mm X 1,14 mm. Le prime larve comparvero il 29 maggio e iniziarono subito a nutrirsi, producendo piccoli fori subcircolari nella pagina inferiore delle foglie, lasciando generalmente intatta quella superiore. Come consuetudine per le larve dei cassidini, i residui delle exuvie, parzialmente ricoperti da

un leggero strato di materia fecale, vennero conservati sulla furca anale, tenuta ripiegata in avanti e sollevata al di sopra del dorso. Se molestate, le larve scuotevano ritmicamente e con energia la furca al di sopra dell'addome. Dopo circa un mese (21 giugno) e quattro mute, le prime larve sgusciate, raggiunte le dimensioni di 4,13 - 4,60 mm, smisero di nutrirsi e si fissarono ad una foglia con una goccia di sostanza vischiosa emessa dall'ano, senza liberarsi dei residui delle mute precedenti, come osservato in altre specie. Dopo poche ore si trasformarono in pupe e la comparsa dei primi adulti si ebbe il 25 giugno. Appena nate, le immagini sono di un giallo chiarissimo, soltanto gli occhi e i palpi labiali sono neri. L'apice dell'ultimo articolo antennale e, in parte, gli altri elementi boccali sono soltanto leggermente offuscati. La superficie dorsale è opaca. Dopo poche ore la colorazione nera interessa anche il labbro superiore. Dopo due giorni l'esoscheletro elitrale è diventato lucido, si evidenziano le bozze juxtascutellari, inzia a vedersi per trasparenza il capo attraverso il pronoto. A questa età il capo è completamente nero, e pure oscurato è il prosterno, compreso il processo prosternale. Più tardi la colorazione scura si estende al mesosterno, al metasterno e, successivamente, alla fascia centrale dell'addome.

Larva di quinta età (Figg. 61 e 66): Larva allungata, a lati debolmente convergenti in direzione caudale a partire dal metatorace; lungo i margini vi sono 16 paia di processi laterali così suddivisi: 4 paia nel protorace, 2 paia nel meso e 2 nel metatorace, 1 paio in ciascun segmento addominale. Ogni processo porta 10-15 spinule di lunghezza variabile e diversamente orientate. La superficie dorsale, escluso il protorace, è solcata da rugosità piuttosto profonde, più o meno sinuose. Colore interamente giallo paglierino. Lunghezza totale, esclusa la furca anale e i processi apicali, 4,60 mm. Larghezza massima (all'altezza del metatorace ed esclusi i processi laterali) 2,56 mm. L'ottavo segmento addominale reca la furca anale, priva di spinule, lunga 2,70 mm. Il complesso dei frammenti delle exuvie e residui fecali applicate sulla furca anale costituisce una struttura del tipo kompakte Kotmaske, sensu Steinhausen (1950).

Capo subcircolare, ipognato. Fronte lievemente depressa nel tratto postero-mediano. Ocelli in numero di 5 per lato, dei quali quattro disposti internamente, in linea leggermente arcuata, il quinto, più piccolo, in posizione latero caudale a detta linea, all'altezza del terzo ocello. Labrum debolmente chitinizzato, con tre paia di setole su ciascun lato e incavo mediano poco accentuato, a fondo rettilineo e lati debolmente angolosi. Antenne bisegmentate, con vari processi sensoriali all'apice, di cui uno maggiore in forma di papilla debolmente conica. Clipeo trasverso, circa 5 volte più largo che lungo. Mandibole con tre denti apicali.

Torace lungo circa 0,75 volte l'addome. Superficie del protorace con vari solchi e rughe, più marcati lateralmente. Scudo protoracico poco evidente, formato da due aree circolari, lievemente depresse, a fondo rugoso portante qualche corta setola. Tali aree risultano separate da una regione mediana rilevata, di superficie più uniforme, con circa 20 setole spiniformi, le maggiori lunghe fino a 0,1 mm, prevalentemente disposte lungo il bordo interno delle aree circolari. Alla base della quarta spina protoracica vi è lo spiracolo anteriore, in una piccola area subtriangolare separata dal corpo del protorace da un solco obliquo. Mesotorace poco meno di quattro volte più largo che lungo, dorsalmente diviso in pre- e post-mesotergite da una linea sinuosa. Metatorace quasi cinque volte più largo che lungo.

Figg. 61-62 - *Cassida subreticulata*: larva al quinto stadio (61) e pupa (62).

Addome con tergiti divisi in pre- e post-tergite da una linea arcuata, più marcata lateralmente. Superficie con numerose piccole setole a disposizione più o meno uniforme. Ai lati dei primi sette pretergiti si trova una coppia di spiracoli addominali, a peritrema molto saliente.

Pupa (Figg. 62 e 66): Lunghezza 4,77 mm. Larghezza 2,98 mm. Colore interamente giallo paglierino, privo di zone pigmentate.

Superficie dorsale opaca, con microrugosità prevalentemente disposta in senso trasversale.

Pronoto circa 3 volte più corto della lunghezza totale del corpo; subpentagonale, convesso; area posteriore più saliente della anteriore. Superficie opaca, con microrugosità variamente disposta; qualche brevissima setola, visibile solo a forte ingrandimento, è presente soprattutto nella metà posteriore. Margine anterolaterale con circa 40 spine di varia lunghezza e per lo più semplici; solo due coppie centro-laterali, più lunghe, portano qualche spinula. Al centro del margine anteriore vi è una intaccatura subtriangolare, dalla quale si diparte una linea liscia, sublucida e leggermente rilevata che attraversa longitudinalmente i due terzi anteriori del pronoto ed è interrotta da una areola trasversale, in forma di una fascia liscia e male delimitata, che costituisce con la linea longitudinale una struttura a croce debolmente rilevata. Margine posteriore bisinuato, con due marcate intaccature sublaterali.

Meso e metatorace privi di particolari strutture ad esclusione degli astucci alari i quali, ruotati lateralmente e ventralmente, sono poco visibili dall'alto.

Tergiti addominali convessi, con linea mediana rilevata quasi in forma di carena; inoltre un solco brevemente inciso, più evidente nei segmenti addominali anteriori, si stacca circa a metà del margine anteriore di ciascun emitergite, raggiungendone la linea mediana. Primi cinque segmenti addominali ciascuno con una coppia di processi laterali in forma di lamine appiattite in senso dorsoventrale. Gli anteriori più ampi, i successivi progressivamente decrescenti in senso caudale. Ciascun processo reca lungo il margine laterale una serie di 7-9 spinule, la apicale sensibilmente più lunga. Alla base di ciascun processo, spostato verso il margine anteriore del tergite, si trova uno spiracolo, con peritrema fortemente saliente. Gli ultimi tre segmenti addominali recano coppie di processi laterali spiniformi, orientati in direzione caudale, solo in parte visibili dall'alto perchè inseriti piuttosto ventralmente.

Fronte marcatamente incavata. Antenne orientate obliquamente verso l'estremità caudale, con segmenti apicali prossimi alla articolazione femoro-tibiale anteriore. Astucci alari sottoposti al piano di giacitura delle zampe anteriori e medie, ma in parte ricoprenti le posteriori, delle quali risultano ben visibili solo tibie e tarsi.

Considerazioni biogeografiche

Le categorie corologiche indicate nel testo sono state individuate secondo i criteri proposti da Vigna Taglianti et al. (1992).

Dall'analisi dei singoli corotipi (Figg. 63-64) emerge una dominanza di elementi ad ampia distribuzione nella regione Paleartica. È però cospiqua anche la presenza di taxa a gravitazione europea, ivi compreso un numero non indifferente di elementi Sudeuropei (17,88% del totale), mentre i taxa riferibili a corotipi Mediterranei rappresentano una percentuale molto modesta (1,3%) delle specie raccolte. È stata esclusa *Leptinotarsa decemlineata* in quanto zoogeograficamente estranea alla fauna paleartica.

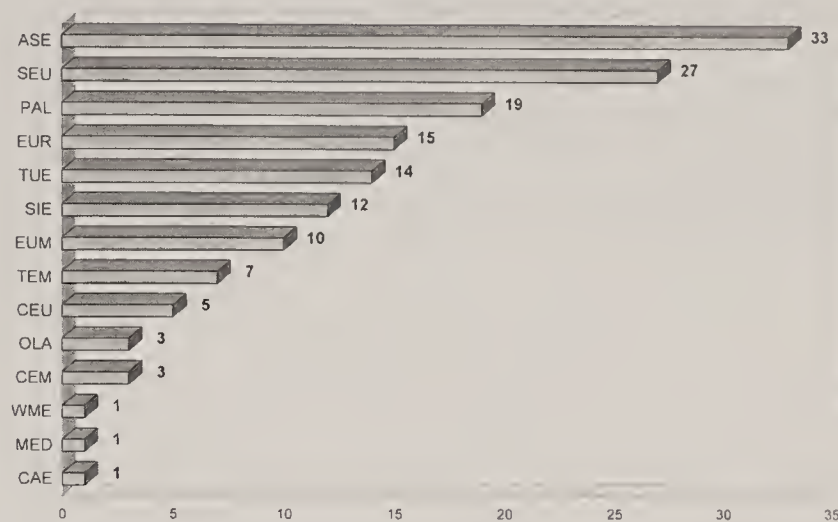



Fig. 63 - Spettro corologico delle specie raccolte.

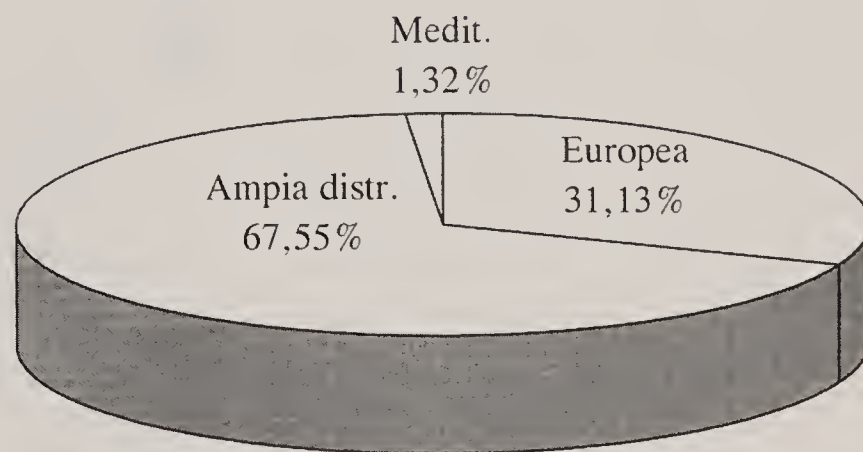



Fig. 64 - Corotipi raggruppati per categorie sintetiche (Vigna Taglianti et al., 1991).

Fenologia

Dalle date di raccolta delle singole specie abbiamo ricavato la Fig. 65, che rappresenta un semplice quadro orientativo dell'abbondanza delle specie nelle raccolte condotte in diversi periodi dell'anno, senza la pretesa di fornire una informazione completa sulla fenologia delle specie.

Per ogni specie sono indicate le stazioni di presenza (st), e per ogni stazione, il numero complessivo degli esemplari raccolti (n) e il numero medio di esemplari raccolti per uscita (F), per il cui calcolo si è tenuto conto solo delle uscite effettuate in periodi in cui la specie è risultata presente.

Le altezze degli elementi di ogni istogramma sono determinate, per ogni specie e per ogni stazione, dal rapporto tra il numero medio di esemplari raccolto nelle uscite effettuate in un particolare periodo e il numero medio (F) di esemplari raccolto nelle uscite effettuate in tutto l'arco dell'anno. In questo modo si ottiene, per ciascun periodo, una misura dell'abbondanza relativa della specie. Per facilitare la lettura di questo dato, i rapporti calcolati sono stati raggruppati in cinque classi di frequenza (<0,5; 0,51-1; 1,01-1,50;

1,51-2; >2), corrispondenti a cinque diverse altezze degli istogrammi.

Abbreviazioni usate nel testo

MM: Museo di Storia Naturale di Milano; CZ: collezione Zoia; Le: lunghezza (distanza apice - base) dell'elitra; Lp: lunghezza del pronoto; lp: larghezza del pronoto; Lt: lunghezza della tibia posteriore in completa distensione; Ld: lunghezza della porzione tibiale posteriore all'inserzione del metatarso; (...) m valore medio di .....

Ringraziamenti

Ringraziamo la Dr.ssa Nicole Berti, del Museo di Storia Naturale di Parigi, per il prestito dei tipi di *Longitarsus anacardius*, e gli amici Serge Doguet, per il prestito di esemplari algerini di *L. anacardius*, David Furth, per il dono di esemplari di *Longitarsus truncatellus* al Museo di Storia Naturale di Milano, e Stefano Zoia, per il dono di esemplari di *Crepidodera peloponnesiaca* al Museo di Storia Naturale di Milano. Un particolare ringraziamento va inoltre al Dr. Giuseppe Panzeri e al Dr. Mauro Villa, rispettivamente Presidente e Direttore del Consorzio Parco Monte Barro, per l'aiuto fornitoci durante le nostre ricerche.

Specie	F	n	st.
Plateum. rustica	0,37	3	9
Oulema duftsch.	0,33	1	1
	0,33	1	6
	0,75	3	8
Crioc. duodecimp.	0,20	1	2
	0,67	2	6
Lilioceris lilii	0,17	1	2
Lilioc. merdigera	0,22	2	2
	0,25	1	8
Labidost. tridentata	0,18	2	2
Labidost. longim.	1,00	3	8
Lachnaia italica	0,29	2	2
	0,33	1	6
Clytra quadrip.	0,27	3	2
	1,50	3	4
	0,57	4	5
	0,33	1	6
Clytra appendic.	0,75	3	4
Clytra laeviusc.	1,00	2	2
	1,00	1	3
	0,20	1	4
	0,25	1	5
	0,71	5	6
	4,00	4	7
	1,67	5	8
	1,57	11	9
Smaragd. salicina	1,14	8	1
	2,74	52	2
	7,55	83	3
	0,25	1	4
	1,92	23	5
	0,50	1	7
	0,33	1	8
	0,50	5	9
Smaragd. flavic.	0,25	2	4
Smaragd. aurita	0,50	1	1
Smaragd. affinis	0,33	1	1
	0,56	10	2
	1,09	12	3
	1,67	25	4
	1,00	12	5
	1,00	6	6
	8,00	8	7
Coptoc. unifasc.	0,75	3	2
	2,00	2	4
	2,00	4	5
Coptoc. scopol.	0,17	1	2
	2,00	2	8
Pachybr. hierogl.	1,81	29	9
Cryptoc. loreyi	0,25	1	8
Cryptoc. coryli	0,40	2	2
	0,33	1	6
Cryptoc. primarius	0,33	1	5
Cryptoc. trimacul.	0,25	1	2
Cryptoc. bipunct.	0,50	1	1
	0,67	10	2
	1,00	9	4
	1,50	15	5
	1,43	10	6
Cryptoc. sericeus	2,00	4	1
	0,33	2	2
	2,42	29	5

Specie	F	n	st.
Cryptoc. sericeus	1,14	8	6
Cryptoc. transiens	2,40	12	1
	1,62	21	2
	1,57	22	3
	3,44	62	4
	4,70	80	5
	2,50	20	6
	8,00	24	7
	2,62	42	9
Cryptoc. nitidus	0,27	4	2
	0,33	1	3
	0,25	1	4
	0,58	7	5
	1,00	10	6
	1,00	1	7
	0,29	2	8
Cryptoc. janthinus	1,25	5	9
Cryptoc. moraei	0,67	4	3
	1,52	32	4
	1,00	1	7
	0,67	2	8
	0,80	12	9
Cryptoc. flavipes	5,15	103	2
	0,20	1	3
	1,07	16	4
	2,00	34	5
	6,00	78	6
	0,67	2	7
	0,25	1	8
Cryptoc. signatifr.	1,00	2	4
	0,33	1	5
	0,91	10	6
	0,43	3	8
Cryptoc. turcicus	1,21	17	2
	1,00	6	6
Cryptoc. bilineatus	2,00	2	1
	1,00	1	2
	4,00	12	5
Cryptoc. elegant.	1,50	6	1
	1,42	17	2
	0,44	4	4
	1,10	11	5
	2,62	21	6
Cryptoc. strigosus	4,00	12	1
	6,67	20	2
	4,89	44	4
	3,44	31	5
	1,14	8	6
	3,50	7	7
	3,50	14	8
	0,4	2	9
Cryptoc. ocellatus	0,31	4	9
Cryptoc. labiatus	1,18	26	2
	0,42	5	4
	7,58	91	5
	3,73	41	6
	1,00	1	7
	1,00	1	8
	1,00	1	9
Cryptoc. vittula	4,50	9	3
	1,00	4	4
	0,75	3	5
	1,00	1	7
Cryptoc. fulvus	0,50	1	5

Specie	F	n	st.
Cryptoc. pusillus	1,00	1	3
	1,78	16	5
Oomorphus conc.	0,25	1	8
Eumolpus asclep.	4,73	38	4
	5,09	56	5
	1,11	10	6
Leptinot. deceml.	0,17	1	2
Chrysol. graminis	1,71	41	9
Chrysol. polita	0,50	1	3
	1,24	21	9
Chrysol. cerealis	0,50	3	2
	1,00	6	3
	0,50	1	5
	0,64	9	6
Chrysol. oricalcia	1,50	3	4
Chrysol. haemopt.	1,00	2	1
	0,50	1	2
	0,40	2	3
	2,17	13	4
	2,00	4	7
	0,33	1	8
Chrysol. rossia	0,33	1	3
Chrysol. marginata	0,50	1	1
	0,90	9	3
Chrysol. fastuosa	1,00	2	4
	0,62	5	9
Gastroph. viridula	0,67	2	3
	0,50	1	6
Phaedon cochl.	0,25	1	9
Hydroth. margin.	0,25	2	9
Plagiod. versicol.	0,50	2	9
Chrysomela populi	0,50	1	4
	0,43	3	6
Timarcha nicaeens.	0,50	1	3
Galeruc. nymph.	0,33	1	9
Galeruc. lineola	0,33	1	9
Galeruc. pusilla	2,11	59	9
Galeruca tanaceti	0,50	1	2
	0,33	1	3
	0,33	1	5
Galeruca pomonae	1,00	1	6
Exos. lusitanicum	1,00	2	1
	0,73	11	2
	0,33	1	3
	0,60	3	4
	0,33	4	5
	6,70	67	6
	4,00	4	7
	0,67	2	8
Calom. circumfusus	0,17	1	2
	6,14	43	6
Lup. longicornis	1,00	3	1
	1,55	31	2
	2,91	32	3
	1,00	13	4
	0,60	9	5
	4,29	60	6
	1,50	6	7
	4,40	22	8
	0,25	2	9
Lup. flavipes	0,44	4	2
	0,25	2	3

Specie F n st.
marzo aprile maggio giugno luglio agosto settembre ottobre novembre
14-30 1-15 16-30 1-15 16-30 1-15 16-30 1-15 16-30 1-15 16-30 1-15 16-30 1-15 16-30 1-15 16-30
Lup. flavipes 0,25 2 5
0,50 3 6
Lup. leonardii 0,20 3 2
0,20 1 4
0,25 1 8
Phyllotr. vittula 0,67 2 1
0,67 1 2
1,50 15 3
1,00 3 4
0,20 1 5
0,45 5 6
1,33 4 7
0,87 7 8
0,25 4 9
Phyllotr. nemorum 0,25 1 4
0,20 1 9
Phyllotr. striolata 0,50 1 1
0,50 1 4
0,33 1 9
Phyllotr. ochripes 2,42 29 3
Phyllotr. aerea 0,40 2 3
0,12 1 9
Aphth. cyparissiae 0,25 1 5
0,57 4 6
Aphth. lutescens 0,25 1 8
1,82 40 9
Aphth. pygmaea 0,25 1 4
Aphth. venustula 4,33 39 1
6,70 114 2
0,50 1 3
4,63 88 4
4,87 73 5
4,28 77 6
3,50 7 7
2,50 20 8
Aphth. coerulea 0,50 1 1
0,50 1 2
1,00 3 3
0,25 1 8
11,4 366 9
Aphth. herbigrada 2,50 30 2
1,44 13 4
9,08 109 5
26,9 564 6
2,00 2 7
Aphth. ovata 0,54 7 6
4,90 49 8
Aphth. atrovirens 0,33 1 6
0,50 1 7
2,86 20 8
Longit. pellucidus 0,50 1 2
0,50 2 8
1,30 30 9
Longit. succineus 2,40 12 1
5,37 86 2
12,7 242 3
3,19 51 4
3,62 47 5
2,57 36 6
10,00 50 7
6,14 43 8

Specie
F
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aprile
maggio
giugno
luglio
agosto
settembre
ottobre
novembre
14-30
1-15 16-30
Longit. succineus 2,37 38 9
Longit. noricus 1,86 13 3
1,00 3 7
2,00 8 8
Longit. rubiginosus 0,50 1 2
0,33 1 3
2,45 27 9
Longit. tabidus 3,06 49 3
Longit. nigrofasc. 1,00 5 1
0,17 1 2
0,50 1 4
0,40 2 9
Longit. lycopi 0,50 1 4
0,25 1 8
4,07 110 9
Longit. helvolus 0,29 2 2
0,50 1 4
15,3 229 6
0,50 1 7
Longit. melanoc. 2,30 23 1
0,20 1 2
0,53 8 3
1,35 23 4
2,00 2 5
1,00 2 7
2,00 12 8
5,25 84 9
Longit. exoletus 1,14 8 2
4,61 106 4
Longit. lewisii 1,00 7 1
0,92 11 3
5,67 34 4
0,75 3 8
0,33 2 9
Longit. pratensis 3,71 26 1
0,55 6 2
8,09 178 3
3,83 92 4
0,43 6 5
10,20 51 6
10,70 107 7
16,70 234 8
1,63 44 9
Longit. longiseta 3,40 17 1
2,95 62 3
0,50 3 4
0,50 1 7
1,00 1 8
Longit. nasturtii 0,33 1 9
Longit. holsaticus 0,67 2 1
0,33 1 9
Longit. luridus 13,7 137 1
2,22 51 2
41,9 922 3
8,71 244 4
1,22 22 5
2,29 32 6
9,10 91 7
19,1 287 8
3,32 103 9
Longit. fulgens 0,60 6 9
Longit. brunneus 2,87 23 1

Specie	F	n	st.
Longit. brunneus	3,75	75	2
	0,33	1	3
	2,71	46	4
	2,24	38	5
	0,90	9	6
	1,00	4	8
Longit. minusculus	0,50	3	8
Longit. niger	2,00	30	4
	1,50	6	7
Longit. pinguis	0,33	1	6
	4,00	16	8
Longit. obliteratus	7,20	144	6
Longit. salviae	3,68	70	3
	1,50	12	6
	2,86	20	7
	13,6	177	8
Altica oleracea	1,78	16	1
	1,19	19	2
	0,57	8	3
	3,14	88	4
	1,36	38	5
	1,42	17	6
	1,43	10	7
	1,00	7	8
	0,51	11	9
Altica carinthiaca	0,80	4	1
	2,06	37	2
	1,25	5	3
	0,67	2	6
Altica impressic.	0,89	8	9
Hermaeoph. merc.	1,25	5	7
	2,17	13	8
Lythraria salicariae	6,67	140	9
Asiorestia brevic.	0,12	1	9
Asiorestia transv.	4,65	121	9
Asiorestia ferrug.	2,10	42	4
	0,50	1	7
	1,50	6	8
	3,00	72	9
Derocrepis sodalis	0,40	2	2
	1,20	12	3
	1,50	9	8
Crepidod. aurea	4,00	12	2
Crepidod. aurata	1,75	35	5
	0,89	24	9
Epitrix pubescens	0,36	4	2
	1,27	14	3
	0,25	1	4
	0,33	1	6
	0,54	7	9
Podagrica fuscic.	33,3	100	1
	0,50	1	2
	4,33	26	3
	0,20	1	6
Mantura obtusata	0,50	1	2
Chaetocn. concinna	0,50	1	3
	0,20	4	9
Chaetocn. laevic.	0,33	1	1
	0,70	7	2
	0,50	1	3
	0,25	1	4
	0,50	5	5
	0,67	2	6
	0,50	1	8
	0,27	3	9
Chaetocn. tibialis	0,33	1	1
	0,20	1	6

Specie	F	n	st.
Chaetocn. conducta	0,40	2	1
	0,64	9	2
	0,82	9	3
	0,85	11	4
	0,77	10	5
	2,79	39	6
	0,67	2	7
	1,00	10	8
	0,86	18	9
Chaetocn. confusa	0,64	7	9
Chaetocn. arida	0,33	1	9
Chaetocn. hortensis	2,87	23	1
	0,75	3	2
	6,50	143	3
	1,39	32	4
	0,92	11	5
	0,58	7	6
	2,63	21	8
	4,00	96	9
Sphaerod. testac.	1,00	1	8
Sphaerod. rubidum	5,22	47	1
	1,24	26	2
	5,59	95	3
	1,57	33	4
	0,56	5	5
	0,50	1	6
	2,83	17	7
	1,89	17	8
Argopus ahrensi	1,50	3	4
Dibolia foersteri	2,47	42	5
Dibolia cryptoceph.	0,33	1	3
	0,54	7	4
	0,41	7	5
Psylliodes affinis	1,00	5	1
	1,33	8	2
	2,56	23	3
	0,56	5	4
	0,25	1	8
	0,40	6	9
Psylliodes napi	0,87	7	3
	0,33	3	4
	0,50	2	8
	0,50	1	9
Psylliodes toelgi	2,60	65	4
	1,11	20	5
	3,00	3	6
	4,57	32	7
Psylliodes brisouti	2,83	17	2
Psylliodes cupreus	5,00	10	4
Psylliodes instabilis	0,47	8	2
Psylliodes dulcam.	0,33	1	1
	1,00	6	2
	1,43	20	3
	0,22	2	4
	0,50	2	8
Cassida subferrug.	0,20	1	2
	1,00	1	3
	0,44	8	9
Cassida viridis	1,00	1	3
	0,20	1	4
	0,13	1	9
Cassida vibex	0,75	3	1
	1,59	27	2
	0,70	10	3

Fig. 65 - Tabella fenologica delle specie raccolte nelle stazioni 1-9.
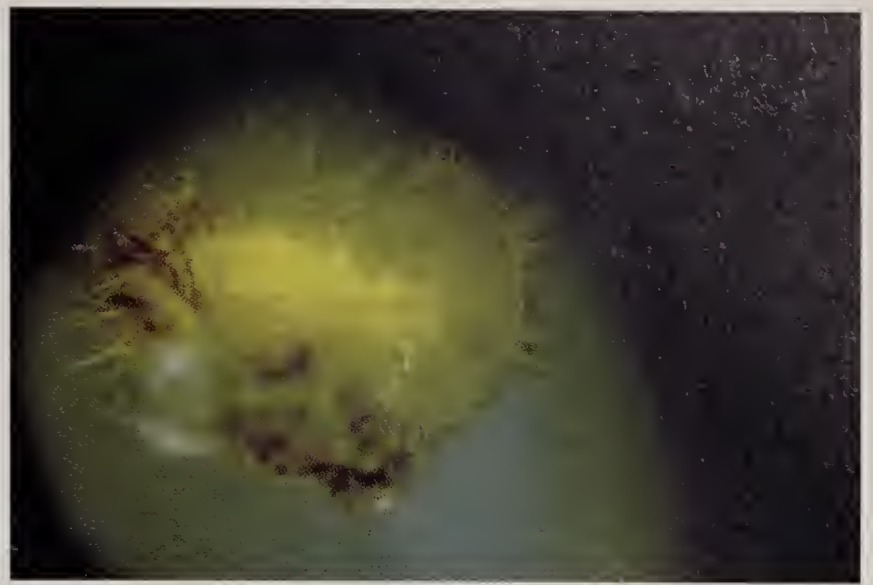
Fig. 66 - *Cassida subreticulata.* a) larva di quinta età con esuvie e residui fecali sulla furca anale; b) larva con furca anale parzialmente ribaltata sul dorso; c) larve coperte dall'ombrello fecale; d) pupa; e) adulti neosfarfallati; f) adulti in accoppiamento.

Fig. 67 - Stazioni di raccolta. a) staz. 1 (in loc. Piani di Barra); b) staz. 2 (in loc. Piani di Barra); c) staz. 5 (Pian Sciresa); d) staz. 6 (superfici prative lungo il sentiero della «cresta occidentale»); e) staz. 7 (in Val di Faè); f) staz. 8 (in Val di Faè).

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I Curculionidi in senso lato (Coleoptera Attelabidae, Apionidae e Curculionidae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Col presente lavoro sono forniti i dati relativi alla popolazione curculionidica del Monte Barro, come risultato di una ricerca condotta negli anni 1989-1992 dal Museo di Storia Naturale di Milano. Le raccolte sono state effettuate prevalentemente in 9 stazioni prative. Vengono analizzate le caratteristiche biogeografiche della popolazione curculionidica, 9 specie (*Nanophyes annulatus, Apion armatum, A. flavimanum, A. filirostre, A. ebeninum, Thamiocolus signatus, Coeliodes dryados, Miarus distinctus, Miarus micros*) sono segnalate come nuove per la Lombardia e si ribadisce la presenza in Italia di *Polydrusus corruscus*.

Abstract - Weevils (Coleoptera Attelabidae, Apionidae and Curculionidae) from Monte Barro (Italy, Lombardy, Lecco).
In the present work data concerning the weevil-fauna of Monte Barro are given, as result of a research carried out by the Natural History Museum of Milano in the years 1989-1992. Samplings have been largely addressed to the study of meadows and 9 sampling sites have been chiefly investigated. The biogegraphic pattern of the weevil-population is analyzed, 9 species (*Nanophyes annulatus, Apion armatum, A. flavimanum, A. filirostre, A. ebeninum, Thamiocolus signatus, Coeliodes dryados, Miarus distinctus, Miarus micros*) are recorded for the first time from Lombardy, and the presence in Italy of *Polydrusus corruscus* is confirmed.

Key words: Monte Barro, Curculionidae, geographic distribution.

Le ricerche effettuate dal Museo di Storia Naturale di Milano nel corso di quattro campagne annuali di raccolta hanno fornito un quadro assai ampio e, nei limiti del possibile, verosimilmente completo della fauna curculionidica del M.Barro. Tale risultato è stato possibile grazie anche agli elementi aggiuntivi che hanno permesso di integrare la già ricca massa di dati prodotta dalle ricerche di Davide Sassi e Carlo Leonardi. Tali elementi sono stati forniti dal lavoro svolto, nell'ambito di una tesi di laurea da me coordinata, dalla Dr.ssa Laura Bonini.

Osservazioni sulle stazioni di raccolta

Le raccolte sono state effettuate prevalentemente in 9 stazioni prative, le cui caratteristiche ambientali sono state ampiamente analizzate nel contributo di Banfi, Galasso & Sassi, in questo stesso volume. Ulteriori stazioni di raccolta, ispezionate soprattutto da Laura Bonini e da Davide Sassi, sono state riunite, nel quadro d'insieme, in una sorta di stazione cumulativa indicata con il numero 10.

Qui di seguito è data una breve descrizione delle stazioni 1-9 e sono indicate le specie esclusive (specificità) per ciascuna stazione; le specie contrassegnate da un asterisco pur non essendo state rinvenute in nessun'altra fra le nove stazioni considerate risultano presenti in uno o più dei biotopi riuniti al numero 10.

Stazione 1: Località Piani di Barra, 610 m, esp. W, interessata da scavi archeologici (Grande Edificio). È caratterizzata da una consistente presenza di prato falciabile che indica una attività di foraggio residua. Specificità: *Lixus bardanae*, *Dorytomus taeniatus*.

Stazione 2: Località Piani di Barra, 600 m, esp. W, interessata da scavi archeologici (Edificio II). Si tratta di una prateria in cui è stata abbandonata la gestione a foraggio, vi è quindi presente un leggero mantello. Specificità: *Attelabus nitens**, *Thamiocolus signatus*, *Coeliodes dryados*, *Tychius longicollis**, *Rhynchaenus signifer**.

Stazione 3: Conca prativa a monte del Monumento dell'Alpino, 630 m, esp. W. Vi si nota la convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale. Specificità: *Coenorhinus aeneovirens**, *Apion confluens*, *Apion flavimanum*, *Apion oblivium*, *Apion holosericeum*, *Phyllobius etruscus**, *Ceuthorhynchus cochleariae*, *Cionus thapsus*.

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion* è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico. Specificità: *Otiorhynchus ovatus*.

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. È un prato arido con montarozzi residui a brughiera; per il resto il livello di base è costituito da prateria a *Brachypodium rupestre* ssp. *caespitosum*. Specificità: *Apion subulatum*, *Sitona suturalis*, *Hypera venusta*, *Micrelus ericae*, *Tychius polylineatus*.

Stazione 6: Superfici prative lungo il sentiero della «Cresta occidentale», che dall'edificio dell'ex sana-

torio sale alla vetta, 750 m, esp. S. Si tratta di una prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura, con forte influsso dell'elemento prenemorale (tendenza a un *Quercetum pubescentis* s. l.) Specificità: *Apion aeneomicans*, *Apion cerdo*, *Apion opeticum*, *Magdalis exarata**, *Tychius junceus*, *Miarus micros*.

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. È una superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8 ma più aperta e con qualche elemento in più di *Mesobromion*. Specificità: *Apion rufirostre, Apion nigritarse, Apion ebeninum, Polydrusus atomarius, Polydrusus corruscus, Hypera nigrirostris, Hypera postica**.

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. È un prato terrazzato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili. Specificità: *Leiosoma concinnum, Trichosirocalus rufulus*.

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Vi si evidenziano tre aspetti essenziali: 1) il canneto, con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto e residui di boscaglia ripariale 2) prato umido oligotrofico (*Molinion coeruleae*); 3) vegetazione erbacea perenne e disorganizzata al margine superiore della stazione. Specificità: *Nanophyes marmoratus, Nanophyes annulatus, Lepyrus capucinus, Hylobius transversovittatus, Rhinoncus perpendicularis, Pelenomus comari, Tapinotus sellatus, Limnobaris t-album, Tychius meliloti, Dorytomus rufatus, Notaris scirpi, Rhynchaenus salicis*.

Elenco delle specie raccolte

In tale elenco si è seguito l'ordine adottato nel recente lavoro di Abbazzi & Osella (1992) sulla curculionidofauna italiana, includendovi le famiglie Attelabidae, Apionidae e Curculionidae. Di tale lavoro sono state seguite nel complesso anche le scelte sistematiche, con l'unica eccezione di rilievo costituita dal mantenimento del senso tradizionale del genere *Apion*, che nel citato lavoro viene suddiviso in 39 generi distinti, ai quali qui viene assegnato invece il rango più tradizionale (e che personalmente ritengo più adeguato nella stragrande maggioranza dei casi) di semplici sottogeneri.

Delle specie censite, 9 risultano nuove per la fauna lombarda.

Lasiorhynchites (Coccigorhynchites) sericeus (Herbst)
Presenza in Italia: tutta Italia e Sicilia.
Piante ospiti: diverse specie del genere *Quercus*.
Due reperti sul versante meridionale verso Sella d. Pila: 13.VI.1990, lg. Bonini (su *Quercus*); 30.V.1990, lg. Sassi (su *Quercus*).

Coenorhinus (Pselaphorhynchites) nanus (Paykull)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Campania, Basilicata, Calabria.
Piante ospiti: in prevalenza salici (*Salix*), ma anche *Betula* e *Alnus*.
Due esemplari raccolti a giugno nelle staz. 2 e 6.

Coenorhinus (Pselaphorhynchites) tomentosus (Gyllenhal)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: in prevalenza salici (*Salix*), più di rado *Populus*.
Due esemplari raccolti a maggio e giugno nelle staz. 2, 4, 5 e 6.

Coenorhinus (s.str.) germanicus (Herbst)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: diverse Salicacee e Rosacee.
Svariati reperti singoli in maggio e giugno nelle stazioni 1, 2, 3, 5, 6, in un prato attiguo alla stazione 4, presso la stazione di osservazione ornitologica e sotto la vetta.

Coenorhinus (s.str.) aeneovirens (Marsham)
Corotipo: Europeo (EUR)
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Trentino -Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Marche, Lazio, Abruzzo, Campania, Puglie.
Piante ospiti : in prevalenza querce (*Quercus*), ma anche Rosacee.
Due esemplari raccolti a maggio nella staz. 3 e in un prato della val Faè vicino alla stazione 7.

Coenorhinus (s.str.) aequatus (Linneo)
Corotipo: Europeo (EUR)
Presenza in Italia: tutta Italia.
Piante ospiti: diverse Rosacee arboree e arbustive.
Due reperti (24.IV.1990, lg. Sassi, boschi della val Faè nei pressi della staz. 7; 13.VI.1990, lg. Bonini, a sud della vetta sopra la stazione di osservazione ornitologica)

Rhynchites (Involvulus) aethiops (Bach)
Corotipo: Europeo (EUR)
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: *Helianthemum nummularium*.
Rinvenuto, spesso in numerosissimi esemplari, sulla sua pianta ospite, nelle stazioni 3, 4, 5 e 6, sopra la stazione di osservazione ornitologica e presso la vetta, fra maggio e luglio, con un marcato picco di maggiore abbondanza in giugno.

Apoderus coryli (Linneo)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: tutta Italia.
Piante ospiti: in prevalenza nocciolo (*Corylus avellana*), ma anche *Alnus* e *Betula*.
Rinvenuto svariate volte, ma in pochi esemplari, nelle stazioni 1, 2, 4, 5, 6 e sul versante meridionale, lungo un sentiero che dall'eremo conduce alla sella della Pila, fra maggio e luglio, con maggiore frequenza in maggio.

Attelabus nitens (Scopoli)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: in prevalenza querce (*Quercus*), ma anche *Castanea*.
Un reperto nella stazione 2 (24.6.1990, lg. Sassi) e uno sul versante meridionale, lungo un sentiero che dall'eremo conduce alla Sella della Pila (30.V.1990, lg. Sassi).

Nanophyes annulatus Aragona
Corotipo: Mediterraneo (MED)
Presenza in Italia: Liguria, Piemonte, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Lazio, Abruzzo, Campania, Calabria, Sicilia. La specie risulta nuova per la Lombardia.
Piante ospiti: *Lythrum salicaria*.
Due soli esemplari provenienti dalla staz. 9, raccolti il 25.V.1990 e il 6.VII.1990.

Nanophyes marmoratus (Goeze)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: tutta Italia.
Piante ospiti: *Lythrum salicaria*.
Numerosi esemplari provenienti dalla staz. 9, raccolti il 24.V.89, il 16.V.1990 ed il 15.VI.1990.

Apion (Ceratapion) armatum Gerstäcker
Corotipo: Centroeuropeo (CEU)
Presenza in Italia: Liguria, Piemonte, Veneto, Friuli-Venezia Giulia, Lazio, Abruzzo, Campania, Calabria. La specie risulta nuova per la Lombardia.
Piante ospiti: *Centaurea* spp.
Numerosi esemplari provenienti dalle stazioni 2, 4, 5 e 7 e sul versante meridionale, ai margini di un sentiero che dall'eremo va alla Sella della Pila, raccolti fra fine aprile (25.IV) e oltre metà settembre (20.IX).

Apion (Ceratapion) onopordi Kirby
Corotipo: Centroasiatico-Europeo (CAE)
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: Asteraceae della tribù Cynareae.
Particolarmente abbondante nella staz. 9, ma rinvenuto anche nelle staz. 1, 2, 3, 4, 5, 8, ai margini di un sentiero a nord-ovest dei Piani di Barra e in un prato presso Camporeso da fine marzo a settembre.

Apion (Diplapion) confluens Kirby
Corotipo: Europeo-Mediterraneo (EUM)
Presenza in Italia: Piemonte, Val d'Aosta, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Toscana, Umbria, Lazio, Puglia, Basilicata, Calabria, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Matricaria* e *Anthemis*.
Due reperti in staz. 3 (9.V.1990, lg. Sassi; 16.V.1991, leg. Bonini).

Apion (Aspidapion) aeneum (Fabricius)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Malva* e *Althaea*.
Alcuni esemplari raccolti nelle stazioni 1, 2 e 3 in maggio e giugno.

Apion (Squamapion) atomarium Kirby
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale, Toscana, Abruzzi, Sardegna.
Piante ospiti: specie del genere *Thymus*.
Alcuni esemplari rinvenuti da maggio a settembre nelle staz. 3, 4 e 5.

Apion (Squamapion) flavimanum Gyllenhal
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Sicilia, Sardegna. La specie risulta nuova per la Lombardia.
Piante ospiti: specie del genere *Mentha*.
Un esemplare proveniente dalla staz. 3 (19.V.1991, lg. Bonini).

Apion (Squamapion) minutissimum Rosenhauer
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Lazio, Toscana.
Piante ospiti: specie del genere *Thymus*.
Tre esemplari, raccolti in differenti località e date: staz. 2, 19.V.1991, lg. Leonardi, staz. 3, 14.III.1990, lg. Leonardi, e in un prato della Val Faè prossimo alla staz. 7, 25.IV.1990, lg. Sassi.

Apion (Squamapion) oblivium Schilsky
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Lombardia.
Piante ospiti: specie del genere *Thymus*.
Un solo esemplare raccolto nella staz. 3 (20.IX.1989, lg. Leonardi).

Apion (Taeniapion) urticarium (Herbst)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: *Urtica dioica*.
Alcuni esemplari raccolti nelle staz. 3, 4 e 9 fra fine marzo e metà giugno.

Apion (Pseudapion) rufirostre (Fabricius)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: *Malva sylvestris* e *neglecta*.
Tre esemplari raccolti nella staz. 7 (V.1992, lg. Sassi).

Apion (Trichopterapion) holosericeum Gyllenhal
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: noto di gran parte d'Italia e Sicilia.
Piante ospiti: *Carpinus betulus* e *orientalis*.
Alcuni esemplari raccolti nella staz. 3 (19.V.1991, lg. Bonini).

Apion (Exapion) difficile Herbst
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Italia settentrionale, Toscana, Lazio, Abruzzi, Puglia, Calabria.
Piante ospiti: specie del genere *Genista*.
Svariati esemplari raccolti fra metà maggio e fine giugno nelle staz. 1, 2, 5 e 6 e ai margini di un sentiero a nord-ovest dei Piani di Barra.

Apion (Exapion) formaneki Wagner
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Italia settentrionale, Toscana, Abruzzi, Campania, Puglia, Basilicata.
Piante ospiti: specie dei generi *Genista* e *Cytisus*.
Svariati esemplari raccolti in maggio e giugno nelle staz. 2, 3, 4, 5 e 6, ai margini di un sentiero a nord-ovest dei Piani di Barra e nei prati sotto la Sella della Pila.

Apion (Protapion) filirostre Kirby
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Liguria, Piemonte, Friuli-Venezia Giulia, Emilia- Romagna, Toscana, Umbria, Lazio, Campania. La specie risulta nuova per la Lombardia.
Piante ospiti: specie del genere *Medicago*.
Due singoli esemplari raccolti nelle stazioni 1 e 7 (rispettivamente il 19.V.1991 ed il 16.V.1990, lg. Leonardi).

Apion (Protapion) nigritarse Kirby
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Un solo esemplare raccolto nella staz. 7 (16.V.1990, lg. Leonardi).

Apion (Protapion) fulvipes Geoffroy
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Trifolium, Medicago* e *Ononis*.
Numerosi esemplari raccolti fra fine aprile e giugno nelle staz. 1, 2, 3, 4, 5, 6. 7 e 9, in un prato vicino alla staz. 7 e in un prato vicino a Camporeso.

Apion (Protapion) trifolii (Linneo)
Corotipo: Paleartco (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Numerosi esemplari raccolti in tutte le stazioni in maggio e giugno.

Apion (Protapion) interjectum Desbrochers
Corotipo: Mediterraneo (MED).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: prevalentemente *Trifolium montanum*; indicata anche *Ononis repens*.
Due singoli esemplari raccolti nelle staz. 2 e 3 (rispettivamente 19.V.1991 e 20.IX.1989, lg. Leonardi).

Apion (Protapion) apricans Herbst
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: *Trifolium pratense*.
Svariati esemplari raccolti fra fine aprile e metà giugno nelle staz. 1-8 e nei boschi della Val Faè.

Apion (Protapion) ononicola Bach
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Ononis*.
Alcuni esemplari raccolti fra metà maggio e giugno nelle staz. 2 e 6, ai margini di un sentiero che dall'eremo porta alla Sella della Pila e nell'area a nord-ovest dei Piani di Barra.

Apion (Protapion) assimile Kirby
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Numerosi esemplari raccolti da marzo a giugno nelle staz. 1-9, ai margini di un sentiero a nord-ovest dei Piani di Barra, in un prato vicino alla staz. 7, in un prato presso Camporeso e in località S.Michele (in un prato attiguo alla stazione 4).

Apion (Protapion) difforme Ahrens
Corotipo: W-Mediterraneo (WME).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Friuli-Venezia Giulia, Toscana, Umbria, Lazio, Basilicata, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Alcuni esemplari raccolti nel staz. 2 e 7 e nei boschi della Val Faè da fine maggio a metà giugno.

Apion (Protapion) varipes Germar
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Alcuni esemplari raccolti nelle staz. 1, 3, 5 e 6 da maggio a settembre.

Apion (Helianthemapion) aciculare Germar
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Liguria, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Abruzzi.
Piante ospiti: specie dei generi *Helianthemum*, *Tuberaria* e *Fumaria*.
Numerosi esemplari raccolti da fine aprile a fine maggio nelle staz. 1, 2 e 5, a Camporeso, in un prato della Val Faè vicino alla staz. 7 e sul versante meridionale, ai margini di un sentiero che dall'eremo conduce alla Sella della Pila.

Apion (Pseudostenapion) simum Germar
Corotipo. Europeo-Mediterraneo (EUM)
Presenza in Italia: Piemonte, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Toscana, Marche, Lazio, Abruzzi, Campania, Basilicata, Sicilia.
Piante ospiti: specie del genere *Hypericum*.
Alcuni esemplari nelle stazioni 2 e 5 in maggio.

Apion (Perapion) curtirostre Germar
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Rumex*.
Numerosi esemplari raccolti nelle staz. 1, 2, 4 e 5 e in un prato attiguo alla staz. 4, fra fine marzo e inizio luglio.

Apion (Perapion) violaceum Kirby
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Rumex*.
Alcuni esemplari raccolti nelle staz. 1, 2, 4 e 5, e in località S.Michele (in un prato attiguo alla stazione 4) da fine marzo a inizio giugno.

Apion (s.str.) cruentatum Walton
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Toscana, Campania, Puglia, Calabria, Sicilia, Sardegna.
Piante ospiti: specie del genere *Rumex*.
Alcuni esemplari raccolti nelle staz. 2, 3, 4, 5, 7, 8 e in località S.Michele (in un prato attiguo alla stazione 4) da fine marzo a settembre.

Apion (Catapion) seniculus Kirby
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: in prevalenza specie del genere *Trifolium*; vi sono però anche indicazioni relative ai generi *Medicago*, *Ononis*, *Vicia* e *Melilotus*.
Numerosi esemplari raccolti quasi ovunque da marzo a settembre.

Apion (Trichapion) simile Kirby
Corotipo: Paleartico (PAL).
Presenza in Italia: Italia settentrionale.
Piante ospiti: *Betula pendula*.
Alcuni esemplari raccolti nelle staz. 2, 4 e 5 fra marzo e luglio.

Apion (Stenopterapion) tenue Kirby
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Medicago*.
Numerosi esemplari raccolti in marzo e aprile nelle staz. 4, 7 e 8 e in località S.Michele (in un prato attiguo alla stazione 4).

Apion (Ischnopterapion) aeneomicans Wencker
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Lombardia, Veneto, Friuli-Venezia Giulia, Umbria, Marche, Sicilia.
Piante ospiti: specie del genere *Dorycnium*.
Un unico reperto: staz. 6 (11.VI.1990, lg. Bonini).

Apion (Ischnopterapion) loti Kirby
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie del genere *Lotus*.
Numerosi esemplari raccolti un po' dovunque (la specie risulta assente solo nelle staz. 8 e 9) da marzo a luglio.

Apion (Ischnopterapion) virens Herbst
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Numerosi esemplari raccolti fra marzo e giugno nelle staz. 1, 3, 4, 7 e 8, in un prato attiguo alla staz. 4, in un prato attiguo alla staz. 7 e in un prato vicino a Camporeso.

Apion (Synapion) ebeninum Kirby
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Abruzzi. La specie risulta nuova per la Lombardia.
Piante ospiti: Fabacee dei generi *Lotus*, *Onobrychis*, *Vicia*, *Astragalus* e *Trifolium*.
Un unico esemplare raccolto nella staz. 7 (23.V.1991, lg. Bonini).

Apion (Holotrichapion) pisi Fabricius
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Medicago*.
Numerosi esemplari raccolti da fine marzo a fine maggio nelle staz. 1, 2, 4, 5, 7 e 9, in un prato attiguo alla staz. 7, in un prato vicino a Camporeso e in località S.Michele (in un prato attiguo alla stazione 4).

Apion (Hemitrichapion) pavidum Germar
Corotipo: Paleartico (PAL).
Presenza in Italia: Italia settentrionale, Toscana, Lazio, Puglia e Sicilia.
Piante ospiti: *Coronilla varia*.
Numerosi esemplari raccolti da marzo a giugno nelle staz. 2 (dove la specie è particolarmente abbondante a metà giugno), 3, 4, 7 e 8, ai margini di un sentiero a nord-ovest dei Piani di Barra e, sul versante meridionale, ai margini di un sentiero che dall'eremo va alla Sella della Pila.

Apion (Cyanapion) gyllenhali Kirby
Corotipo: Europeo (EUR).
Presenza in Italia: segnalato di gran parte delle regioni Italiane e di Sicilia, ma non ancora noto di Lombardia.
Piante ospiti: specie del genere *Vicia*.
Un unico esemplare raccolto nella staz. 2 (16.V.1991, lg. Bonini).

Apion (Oxystoma) cerdo Gerstäcker
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Vicia*.
Un unico esemplare raccolto nella staz. 6 (23.V.1991, lg. Bonini).

Apion (Oxystoma) subulatum Kirby
Corotipo: W-Paleartico (WPA).
Presenza in Italia: noto di gran parte d'Italia e Sicilia.
Piante ospiti: specie del genere *Lathyrus*.
Un unico esemplare raccolto nella staz. 5 (23.V.1991, lg. Bonini).

Apion (Oxystoma) opeticum Bach
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Basilicata, Calabria e Sicilia.
Piante ospiti: *Lathyrus vernus*.
Un unico esemplare raccoilto nella staz. 6 (23.V.1991, lg. Bonini)

Apion (Eutrichapion) gribodoi Desbrochers
Corotipo: S-Europeo (SEU).
Presenza in Italia: Piemonte, Lombardia, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Lazio, Campania, Basilicata e Calabria.
Piante ospiti: *Galega officinalis*.
Due esemplari raccolti a nord-ovest dei Piani di Barra (23.VI.1991, lg. Bonini).

Apion (Eutrichapion) ervi Kirby
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Lathyrus* e *Vicia*.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2, 3, 6, 7 e 8, ai margini di un sentiero a nord-ovest dei Piani di Barra e in un prato presso Camporeso.

Apion (Eutrichapion) viciae Paykull
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Lathyrus* e *Vicia*.
Alcuni esemplari raccolti in maggio nelle staz. 2, 3, 6 e 7 e in un prato presso Camporeso.

Otiorhynchus (s.str.) salicicola Heyden
Corotipo: Alpino.
Presenza in Italia: Italia settentrionale, Toscana.
Piante ospiti: specie verosimilmente polifaga.
Alcuni esemplari raccolti nelle staz. 3, 4, 7, 8 e nei boschi della Val Faé in maggio e giugno.

Otiorhynchus (s.str.) vehemens Boheman
Corotipo: Alpino.
Presenza in Italia: Alpi e Prealpi occidentali, Appennino settentrionale.
Piante ospiti: specie verosimilmente polifaga.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 2, 3, 6, 7 e 8, nei prati sotto Sella della Pila (m 700) e nei boschi della Val Faè.

Otiorhynchus (s. str.) ***frescati*** Boheman
Corotipo (SEU)
Presenza in Italia: Italia settentrionale e centrale, Campania.
Piante ospiti: specie polifaga.
Un esemplare raccolto nella staz. 9 (15.VI.1990, lg. Sassi) e uno in un prato della Val Faè vicino alla staz. 7 (25.IV.1990, lg. Sassi).

Otiorhynchus (Dorymerus) carmagnolae Villa
Corotipo: Alpino.
Presenza in Italia: Alpi e Prealpi biellesi e lombarde.
Piante ospiti: specie verosimilmente polifaga.
Alcuni esemplari raccolti nelle staz. 2 e 5 e nei boschi della Val Faè in giugno e luglio.

Otiorhynchus (Tournieria) ovatus (Linneo)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Abruzzi.
Piante ospiti: specie polifaga.
Un unico reperto (staz. 4, 30.V.1989, lg. Sassi).

Homorhythmus hirticornis (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie polifaga.
Numerosi esemplari raccolti in maggio e giugno nelle staz. 1, 2, 5, 6 e 7, ai margini di un sentiero a nord-ovest dei Piani di Barra e nei boschi della Val Faè.

Phyllobius (Parnemoicus) subdentatus Boheman ssp.***roboretanus*** Gredler
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale.
Piante ospiti: Salicacee e Rosacee.
Numerosi esemplari raccolti nelle staz. 2, 3, 5, 6 e 9 e nei prati sotto Sella d. Pila (m 700) in maggio e giugno.

Phyllobius (Parnemoicus) chloropus (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: Valle d'Aosta, Piemonte, Lombardia, Trentino-Alto Adige, Emilia-Romagna, Toscana, Marche, Abruzzi, Lazio, Campania, Basilicata.
Piante ospiti: *Alnus glutinosa* e *viridis*.
Alcuni esemplari raccolti in maggio nelle staz. 1, 6 e 7 e nei boschi della Val Faè.

Phyllobius (s.str.) virideaeris Laicharting ssp.*padanus* Pesarini
Corotipo: Alpino.
Presenza in Italia: Italia settentrionale.
Piante ospiti: Salicacee.
Alcuni esemplari raccolti nelle staz. 1, 2, 3 e 5 in maggio e giugno.

Phyllobius (s.str.) pyri (Linneo) ***s. str.***
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: la sottospecie nominale è diffusa in tutta l'Italia settentrionale e centrale.
Piante ospiti: Rosacee arboree o arbustive.
Numerosissimi esemplari raccolti un po' dovunque (la specie non è stata rinvenuta solamente nella staz. 4) da aprile a giugno.

Phyllobius (s.str.) etruscus Desbrochers
Corotipo: Alpino-Appenninico.
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: Rosacee e Salicacee.
Alcuni esemplari raccolti in aprile e maggio nella staz. 3 e in un prato della Val Faè vicino alla staz. 7.

Phyllobius (Dieletus) argentatus (Linneo) ***s.str.***
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia.
Piante ospiti: Rosacee.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 2, 3, ai margini di un sentiero a nord-ovest dei Piani di Barra e nei boschi della Val Faè.

Polydrusus (Metallites) marginatus Stephens
Corotipo: W-Europeo (WEU).
Presenza in Italia: tutta Italia
Piante ospiti: Rosacee.
Un esemplare raccolto nei boschi della Val Faè (30.V.1990, lg. Bonini).

Polydrusus (Metallites) atomarius (Olivier)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni alpine e Appennino settentrionale.
Piante ospiti: Conifere.
Un esemplare raccolto nella staz. 7 (22.VI.1992, lg. Leonardi).

Polydrusus (Tylodrusus) corruscus Germar, Figg. 1, 5
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Toscana.

Fig. 1 - *Polydrusus corruscus* Germar, ♂.

Piante ospiti: specie del genere *Salix*.

Un esemplare raccolto nella staz. 7 (23.V.1991, lg. Bonini).

Osservazioni: singolarmente, questa specie risulta esclusa dalla fauna italiana nel citato lavoro di Abbazzi & Osella (1992), a dispetto delle precedenti segnalazioni di svariati autori. Tale esclusione non è da attribuirsi ad una semplice svista, poiché essa viene esplicitamente ribadita nel successivo lavoro di Abbazzi, Osella, Calamandrei & Altea (1993), in cui *P. corruscus* è elencato fra le specie che si ritengono erroneamente segnalate d'Italia. Oltre al reperto relativo al M. Barro, ho personalmente raccolto in serie questa specie anche nei dintorni di Lodi lungo la sponde del fiume Adda su *Salix* (9.V.65). Essa si può distinguere agevolmente dagli affini *P. pterygomalis* Boheman e *P. flavipes* (Degeer) in base ai seguenti caratteri, già sottolineati in parte da precedenti autori:

1 Porzione dorsale delle tempie fortemente ed angolosamente rilevata a ciascun lato, occhi relativamente grandi e poco convessi (Fig. 3). Elitre con pubescenza biancastra discretamente lunga e densa, sollevata in modo netto anche nella porzione basale .... *pterygomalis* Boheman

– Porzione dorsale delle tempie debolmente e non angolosamente rilevata, occhi più piccoli e convessi (figg. 4, 5). Pubescenza elitrale, nella porzione basale, pressoché totalmente coricata 2

2 Elitre con pubescenza formata da peli nerastri nettamente sollevati sulla porzione apicale. Occhi discretamente ma non fortemente convessi, a convessità uniforme (Fig. 4) .... *flavipes* (Degeer)

– Elitre con pubescenza formata da peli biancastri totalmente coricati su tutta la superficie. Occhi fortemente convessi, a convessità leggermente irregolare (Fig. 5) .... *corruscus* Germar

Polydrusus (Tylodrusus) pterygomalis Boheman, Figg. 2, 3

Corotipo: sibirico-europeo (SIE).

Presenza in Italia: tutta Italia

Piante ospiti: diverse specie arboree di Fagales.

Un esemplare raccolto nei boschi della Val Faè (23.V.1991, lg. Sassi).

Polydrusus (Eustolus) cervinus (Linneo)

Corotipo: Sibirico-Europeo (SIE).

Presenza in Italia: tutta Italia, Sicilia.

Piante ospiti: specie rizofaga allo stato larvale su *Dactylis glomerata*.

Numerosi esemplari raccolti in maggio e giugno nelle staz. 2, 3, 4, 5 e 6 e sul versante meridionale, ai margini di un sentiero che dall'eremo va alla Sella della Pila.

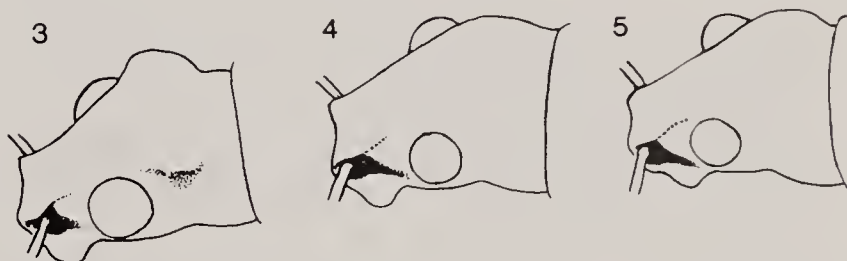
Polydrusus (Eustolus) confluens Stephens

Corotipo: Europeo (EUR).

Presenza in Italia: Piemonte, Lombardia, Friuli-Venezia Giulia, Emilia-Romagna.

Piante ospiti: specie dei generi *Cytisus*, *Ulex* e *Genista*.

Alcuni esemplari raccolti nelle staz. 1, 3 e 5 in maggio.

Fig. 2 - *Polydrusus pterygomalis* Boheman, ♂.

Figg. 3-5 - Capo visto di tre quarti di: 3) *Polydrusus pterygomalis* Boheman; 4) *P. flavipes* (Degeer) e 5) *P. corruscus* Germar.

Polydrusus (Thomsoneonymus) sericeus (Schaller)

Corotipo: Europeo (EUR).

Presenza in Italia: tutta Italia

Piante ospiti: specie polifaga.

Numerosi esemplari raccolti in tutte le stazioni (ad eccezione delle staz. 1 e 8) da fine aprile a metà giugno.

Liophloeus (s.str.) tessulatus (Müller) ***s.str.***

Corotipo: Centroeuropeo (CEU).

Presenza in Italia: Piemonte, Valle d'Aosta, Lombardia, Veneto, Trentino-Alto Adige.

Piante ospiti: *Heracleum sphondylium*.

Due esemplari (staz. 5, 30.V.1991, lg. Leonardi, e staz. 8, 16.V.1990, lg. Sassi).

Stasiodis parvulus (Fabricius)

Corotipo: Alpino-Appenninico.

Presenza in Italia: Liguria, Piemonte, Lombardia, Trentino-Alto Adige, Emilia-Romagna, Toscana, Umbria, Abruzzi.

Piante ospiti: *Trifolium repens*.
Numerosissimi esemplari raccolti in gran parte delle stazioni (la specie non è stata rinvenuta nelle staz. 7 e 9) in maggio e giugno.

Sciaphilus asperatus (Bonsdorff)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Toscana.
Piante ospiti: *Primula officinalis*.
Un singolo esemplare raccolto nei boschi della Val Faé (11.VI.1991, lg. Bonini).

Strophosoma (s.str.) melanogrammum (Forster)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sardegna.
Piante ospiti: specie polifaga.
Numerosi esemplari raccolti a fine aprile e maggio nelle staz. 1, 2, 5 e nei boschi della Val Faè.

Barynotus obscurus (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie polifaga.
Alcuni esemplari raccolti a maggio nelle staz. 2 e 6.

Sitona (s.str.) tibialis (Herbst)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia.
Piante ospiti: specie dei generi *Cytisus*, *Genista* e *Ulex*.
Alcuni esemplari raccolti da fine marzo a fine maggio nelle staz. 5 e 6, inoltre ai margini di un sentiero che va dall'eremo alla Sella d. Pila e in un prato della Val Faè vicino alla staz. 7.

Sitona (s.str.) suturalis Stephens
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia.
Piante ospiti: specie dei generi *Vicia* e *Lathyrus*.
Un singolo esemplare raccolto nella staz. 5 (30.V.1991, lg. Leonardi).

Sitona (s.str.) sulcifrons (Thunberg) ssp.***argutulus*** Gyllenhal
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutta Italia.
Piante ospiti: specie dei generi *Trifolium* e *Medicago*.
Numerosi esemplari raccolti in tutte le stazioni da marzo a settembre.

Sitona (s.str.) flavescens (Marsham)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia.
Piante ospiti: Papilionacee, soprattutto dei generi *Trifolium* e *Medicago*.
Un esemplare raccolto nella staz. 5 (10.VI.1991, lg. Bonini) e uno nella staz. 9 (15.VI.1990, lg. Sassi).

Sitona (s.str.) puncticollis Stephens
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: Papilionacee, soprattutto del genere *Trifolium*.
Due esemplari raccolti il 10.VI.1991 nella staz. 1 (lg. Leonardi) e nella staz. 2 (lg. Bonini).

Sitona (s.str.) humeralis Stephens
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia.
Piante ospiti: Papilionacee, soprattutto del genere *Medicago*.
Alcuni esemplari raccolti nelle staz. 4, 5, 7, 9 e in Località San Michele (in un prato attiguo alla stazione 4) da fine marzo a giugno.

Sitona (s.str.) hispidulus (Fabricius)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia.
Piante ospiti: Papilionacee.
Alcuni esemplari raccolti nelle staz.1, 3, 7, 8 e in località San Michele (in un prato attiguo alla stazione 4) da marzo a giugno.

Pseudocleonus cinereus (Schrank)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: diverse Asteracee.
Un esemplare raccolto in un prato della Val Faé prossimo alla staz. 7 (6.V.1990, lg. Sassi) e un altro nei prati sotto Sella della Pila (m 700) (30.V.1990, lg. Sassi).

Pseudocleonus grammicus (Panzer)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale.
Piante ospiti: *Centaurea jacea*.
Un esemplare raccolto nella staz. 2 (25.VIII.1992, lg. Sassi) ed uno nella staz. 3 (10.X.1991, lg. Leonardi).

Lixus (Dilixellus) bardanae (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia.
Piante ospiti: specie del genere *Rumex*.
Un unico reperto (staz. 1, 9.VI.1991, lg. Sassi)

Larinus (Larinorhynchus) sturnus (Schaller)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Cirsium*, più di rado *Carduus* e *Centaurea*.
Alcuni esemplari raccolti nelle staz. 2, 3 e 9 da maggio a ottobre.

Larinus (Larinomesius) obtusus Gyllenhal
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie del genere *Centaurea*.
Numerosi esemplari raccolti da maggio a settembre nelle staz. 1, 2, 3, 5, 6, ai margini di un sentiero a nord-ovest dei Piani di Barra e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

Hypera zoilus (Scopoli)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Trifolium* e *Medicago*.
Tre esemplari raccolti nelle staz. 2, 3 e in località San Michele (in un prato attiguo alla stazione 4) da giugno a ottobre.

Hypera vidua (Gené), Fig. 6
Corotipo: Alpino.
Presenza in Italia: Liguria, Piemonte, Lombardia, Trentino-Alto Adige, Toscana.
Piante ospiti: specie del genere *Geranium*.

Fig. 6 - *Hypera vidua* (Gené), ♂, habitus.

Quattro esemplari raccolti nella staz. 2 (10.III.1991, lg. Leonardi, 14.III.1990 e 10.X.1991 lg. Sassi) e un esemplare nella staz. 5 (18.VI.1991, lg. Sassi).

Hypera nigrirostris (Fabricius)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia.
Piante ospiti: specie dei generi *Trifolium* e *Ononis*.
Un esemplare raccolto nella staz. 7 (23.V.1991, lg. Bonini).

Hypera postica (Gyllenhal)
Corotipo: Olartico (OLA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie dei generi *Trifolium* e *Medicago*.
Due esemplari raccolti il 25.IV.1990 (lg. Sassi) nella staz. 7 e in un prato attiguo alla stessa.

Hypera venusta (Fabricius)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose specie di Papilionacee.
Quattro esemplari raccolti nella staz. 5 (16.V.1990 e 8.VII.1990, lg. Leonardi e Sassi).

Donus oxalidis (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale.
Piante ospiti: *Petasites* e *Adenostyles*.
Un esemplare raccolto nella staz. 2 (12.VII.1992, lg. Sassi), uno nella staz. 7 (23.V.1991, lg. Bonini), alcuni esemplari nel bosco sottostante al monumento dell'Alpino e un altro nei boschi della val Faè.

Donus intermedius (Boheman)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Piemonte, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche.
Piante ospiti: specie del genere *Mentha*.
Due esemplari raccolti nella staz. 1 (18.VI.1991 e 10.X.1991, lg. Sassi), uno nella staz. 2 (12.VII.1991, lg. Sassi) ed uno nella staz. 4 (10.X.1990, lg. Leonardi).

Limobius borealis (Paykull)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Geranium*.
Numerosissimi esemplari raccolti nelle staz. 1, 2, 4, 5 e 6 da marzo a giugno.

Lepyrus capucinus (Schaller)
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Toscana, Lazio.
Piante ospiti: specie polifaga.
Alcuni esmplari raccolti in giugno nella staz. 9.

Hylobius (Hylobitelus) transversovittatus (Goeze)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Trentino-Alto Adige, Emilia-Romagna, Toscana, Lazio, Campania, Basilicata, Sicilia.
Piante ospiti: *Lythrum salicaria*.
Alcuni esemplari raccolti nella staz. 9 nei mesi di maggio, giugno, settembre e ottobre (lg. Sassi).

Liparus (s.str.) dirus (Herbst)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Italia settentrionale e centrale.
Piante ospiti: specie del genere *Laserpitium*.
Numerosi esemplari raccolti a maggio nelle staz. 2, 5, 6 e 7, inoltre presso la vetta e lungo un sentiero che dall'eremo va alla Sella della Pila.

Leiosoma concinnum Boheman
Corotipo: Alpino.
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Toscana, Marche.
Piante ospiti: biologia sconosciuta.
Due esemplari raccolti nella staz. 8 (25.IV.1990, lg. Sassi e 16.V.1990, lg. Bonini).

Magdalis (Neopanus) cerasi (Linneo)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: Rosacee arboree ed arbustive.
Alcuni esemplari raccolti a maggio nelle staz. 8 e 9 e sul versante meridionale, ai margini di un sentiero che dall'eremo va alla Sella della Pila.

Magdalis (Neopanus) exarata Brisout
Corotipo: Europeo (EUR).
Presenza in Italia: nota di gran parte delle regioni d'Italia e di Sicilia, ma non mancora segnalata per la Lombardia.
Piante ospiti: specie del genere *Quercus*.
Alcuni esemplari raccolti a maggio nella staz. 6 e sotto la vetta del M.Barro

Acalles lemur (Germar)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Calabria.
Piante ospiti: specie polifaga.
Un unico esemplare raccolto nel sottobosco della Val Faé (21.IX.1992).

Echinodera (Ruteria) hypocrita (Boheman)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie polifaga.
Due reperti (staz. 7, 21.V.1991, lg. Bonini; staz. 8, 25.V.1990, lg. Sassi)).

Mononychus punctumalbum (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: *Iris pseudacorus.*
Svariati esemplari raccolti in maggio e giugno nelle staz. 6 e 9.

Rhinoncus (s.str.) bruchoides (Herbst)
Corotipo: Paleartico (PAL).
Presenza in Italia: noto di gran parte dell'Italia settentrionale e centrale, Campania, Basilicata e Sardegna.
Piante ospiti: specie del genere *Polygonum.*
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2 e 4.

Rhinoncus (s.str.) pericarpius (Linneo)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Rumex.*
Alcuni esemplari raccolti a maggio nelle staz. 1, 2, 4, 5 e 9.

Rhinoncus (Amalorhinoncus) perpendicularis (Reiche)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Polygonum.*
Un unico reperto (staz. 9, 15.VI.1990, lg. Sassi).

Pelenomus comari (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Toscana.
Piante ospiti: svariate piante di diverse famiglie: *Lythrum salicaria, Comarum palustre, Alchemilla vulgaris, Sanguisorba officinalis, Polygonum persicaria.*
Un unico reperto (staz. 9, 30.III.1990, lg. Leonardi).

Tapinotus sellatus (Fabricius)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Lazio.
Piante ospiti: *Lysimachia vulgaris.*
Un unico reperto (staz. 9, 15.VI.1990, lg. Sassi).

Ceutorhynchus (s.str.) floralis (Paykull)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: svariate Brassicacee, ma soprattutto *Capsella bursa-pastoris.*
Alcuni esemplari raccolti nelle staz. 1-5, da fine marzo a maggio.

Ceutorhynchus (s.str.) erysimi (Fabricius)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: svariate Brassicacee, ma soprattutto *Capsella bursa-pastoris.*
Alcuni esemplari raccolti nelle staz. 1, 2, 3 e 4, presso l'Osservatorio ornitologico e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

Ceutorhynchus (s.str.) contractus (Marsham)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: numerose specie di svariate famiglie, soprattutto Brassicaee e Resedacee.
Numerosi esemplari raccolti nelle staz. 3, 4, 5, 7 e 8 da fine marzo a giugno.

Ceutorhynchus (s.str.) cochleariae (Gyllenhal)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: noto di gran parte d'Italia settentrionale e centrale, Basilicata.
Piante ospiti: numerose specie di Brassicacee.
Due reperti in staz. 3 (9.V.1990, lg. Sassi; 16.V.1991, lg. Bonini).

Ceutorhynchus (Glocianus) punctiger (Gyllenhal)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia.
Piante ospiti: *Taraxacum officinale.*
Alcuni esemplari raccolti nelle staz. 1, 2, 3 e 8 in marzo e maggio.

Ceutorhynchus (Glocianus) distinctus Brisout
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: Asteracee dei generi *Hypochoeris, Crepis, Lactuca* e *Hieracium.*
Alcuni esemplari raccolti a maggio nelle staz. 1, 2, 3 e 5.

Nedyus quadrimaculatus (Linneo)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: *Urtica dioica.*
Alcuni esemplari raccolti in maggio e giugno nelle staz. 2, 3, 5 e 9 e nei boschi della Val Faè.

Thamiocolus signatus (Gyllenhal)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Liguria, Piemonte, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Lazio. La specie risulta nuova per la Lombardia.
Piante ospiti: *Stachys recta.*
Alcuni esemplari raccolti nella staz. 2 tra il 23.V e il 10.VI.

Trichosirocalus rufulus (Dufour)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Lombardia, Emilia-Romagna, Toscana, Italia meridionale, Sicilia.
Piante ospiti: specie del genere *Plantago.*
Un unico reperto (staz. 8, 14.III.1990, lg. Leonardi).

Trichosirocalus troglodytes (Fabricius)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.

Piante ospiti: *Plantago lanceolata*.
Alcuni esemplari raccolti da marzo a maggio nelle staz. 3, 5 e 8.

Micrelus ericae (Gyllenhal)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana.
Piante ospiti: *Calluna vulgaris*.
Numerosi esemplari raccolti nella staz. 5 fra il 16.V e il 10.VI.

Zacladus geranii (Paykull)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Geranium*.
Numerosissimi esemplari raccolti in maggio e giugno nelle staz. 1, 2, 4, 5, 6, 7, 8 e 9, presso l'Osservatorio ornitologico, a Camporeso, ai margini di un sentiero a nord-ovest dei Piani di Barra e nei boschi della Val Faè.

Coeliodes dryados (Gmelin)
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Trentino-Alto Adige, Emilia-Romagna, Toscana, Umbria, Campania, Puglia. La specie risulta nuova per la Lombardia.
Piante ospiti: *Quercus robur* e *petraea*.
Un unico reperto (staz. 2, 3.IV.1991, lg. Bonini).

Orobitis cyaneus (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Toscana, Lazio, Abruzzi, Campania, Calabria.
Piante ospiti: specie del genere *Viola*.
Un unico esemplare raccolto nei boschi della Val Faè (25.IV.1990, lg. Sassi).

Baris scolopacea Germar
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Toscana, Lazio, Campania, Sicilia, Sardegna.
Piante ospiti: Chenopodiacee.
Due soli reperti (staz 4, 8.VII.1990, lg. Sassi e staz. 5, 28.V.1990, lg. Bonini).

Limnobaris t-album (Linneo)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia.
Piante ospiti: Ciperacee.
Alcuni esemplari raccolti nella staz. 9 da marzo a giugno.

Anthonomus (s.str.) rubi (Herbst)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia.
Piante ospiti: numerose specie di Rosacee.
Numerosi esemplari raccolti da aprile a giugno nelle staz. 1, 2, 3, 4, 5, 6, 8, 9 e sul versante meridionale, ai margini di un sentiero che va dall'eremo alla Sella della Pila.

Curculio glandium Marsham
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Quercus*.
Alcuni esemplari raccolti in aprile e maggio nelle staz. 2 e 5.

Curculio nucum Linneo
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia.
Piante ospiti: *Corylus avellana*.
Alcuni esemplari raccolti da maggio a luglio nelle staz. 2 e 5.

Balanobius pyrrhoceras (Marsham)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: parassita di galle di Cinipidi su querce.
Alcuni esemplari raccolti nelle staz. 2, 5 e 6 e in un prato della Val Faè vicino alla staz. 7.

Tychius (s.str.) meliloti Stephens
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Melilotus*.
Alcuni esemplari raccolti fra il 9.V e l'11.VI nella staz. 9.

Tychius (s.str.) polylineatus (Germar)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Un unico reperto (staz. 5, 23.V.1991, lg. Bonini).

Tychius (s.str.) schneideri (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: *Anthyllis vulneraria*.
Alcuni esemplari raccolti in maggio nelle staz. 5 e 6.

Tychius (s.str.) junceus (Reich)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: noto di gran parte dell'Italia settentrionale e centrale, Basilicata, Sicilia.
Piante ospiti: specie dei generi *Trifolium* e *Melilotus*.
Un unico reperto (staz. 6, 23.V.1991, lg. Bonini).

Tychius (s.str.) stephensi Schönherr
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: Specie del genere *Trifolium*, soprattutto *T.pratense*.
Numerosi esemplari raccolti nelle staz. 1, 2, 3, 4, 5, 6, 8 e 9 e nei boschi della Val Faè.

Tychius (s.str.) longicollis Brisout
Corotipo: S-Europeo (SEU).
Presenza in Italia: tutta Italia.
Piante ospiti: *Ononis repens*.
Alcuni esemplari raccolti a maggio nella staz. 2 e nei boschi della Val Faè.

Tychius (s.str.) picirostris (Fabricius)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*, soprattutto *T.repens*.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 3 e 5.

Tychius (s.str.) cuprifer (Panzer)
Corotipo: W-Paleartico (WPA).

Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Trifolium*.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2, 3 e 5 e in un prato presso Camporeso.

Sibinia viscariae (Linneo)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie dei generi *Silene* e *Lychnis*.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2, 3, 4 e 7.

Sibinia pellucens (Scopoli)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia.
Piante ospiti: *Lychnis dioica*.
Alcuni esemplari raccolti da maggio a luglio nelle staz. 2, 3, 4 e 5 e nei boschi della Val Faè.

Dorytomus (s.str.) taeniatus (Fabricius)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: Salicacee.
Alcuni esemplari raccolti in maggio e giugno nella staz. 1.

Dorytomus (Olamus) rufatus (Bedel)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Trentino-Alto Adige, Emilia- Romagna, Toscana, Abruzzi, Molise.
Piante ospiti: specie del genere *Salix*.
Numerosi (25) esemplari raccolti nella staz. 9 (16.V.1990, lg. Leonardi). Oltre a questa serie, la specie è stata raccolta nella medesima stazione solo in tre esemplari (25.V.1990, lg. Sassi e 19.V.1991, lg. Leonardi), il che indica come la specie presenti verosimilmente una comparsa massiccia e di breve durata, discontinua da un anno all'altro.

Notaris (s.str.) scirpi (Fabricius)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Emilia-Romagna, Toscana, Umbria, Abruzzi, Molise, Basilicata, Calabria, Sicilia.
Piante ospiti: *Carex paludosa*.
Un unico reperto (staz. 9, 25.V.1990, lg. Sassi).

Pachytychius (s.str.) sparsutus (Olivier)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie dei generi *Cytisus*, *Genista* e *Ulex*.
Numerosi esemplari raccolti in maggio e giugno nelle staz. 5 e 6, inoltre lungo un sentiero a nord-ovest dei Piani di Barra e nei prati intorno alla Sella d. Pila.

Rhynchaenus (s.str.) rufus (Schrank)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Lazio, Basilicata, Sardegna.
Piante ospiti: *Ulmus campestris*.
Un esemplare raccolto presso l'Osservatorio ornitologico (13.VI.1990, lg. Bonini) e uno nei prati verso Sella della Pila (6.VII.1990, lg. Sassi).

Rhynchaenus (Alyctus) signifer (Creutzer)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia.
Piante ospiti: specie del genere *Quercus*, soprattutto *Q. robur*.
Due esemplari raccolti nella staz. 2 (15.VI.1990, lg. Leonardi), uno nei prati sotto la Sella d. Pila (30.V.1990, lg. Sassi), e uno ai margini di un sentiero che dall'eremo porta alla Sella della Pila (30.V.1990).

Rhynchaenus (Tachyerges) salicis (Linneo)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia.
Piante ospiti: specie del genere *Salix*, soprattutto *Salix cinerea*.
Un esemplare raccolto nella staz. 9 (24.VI.1989, lg. Sassi).

Rhamphus pulicarius (Herbst)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Salix*.
Due esemplari raccolti sul versante meridionale, sotto Sella d. Pila (m 700) (6.V.1990 e 30.V.1990, lg. Sassi).

Mecinus janthinus (Germar)
Corotipo: Europeo (EUR).
Presenza in Italia: Noto di gran parte d'Italia, Sicilia.
Piante ospiti: specie del genere *Linaria*.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 2, 5 e 9.

Mecinus pyraster (Herbst)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: *Plantago lanceolata*.
Alcuni esemplari raccolti da marzo a giugno nelle staz. 3, 4, 5 e 9 e nei boschi della Val Faè.

Mecinus circulatus (Marsham)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Plantago*, soprattutto *P. lanceolata*.
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 9 e nei boschi della Val Faè.

Miarus (Miaromimus) graminis (Gyllenhal)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: noto di gran parte d'Italia.
Piante ospiti: specie del genere *Campanula*.
Alcuni esemplari raccolti in maggio nelle staz. 2, 5, 6, 8 e 9 e in un prato presso Campòreso.

Miarus (Miaromimus) distinctus (Boheman)
Corotipo: Alpino-Appenninico.
Presenza in Italia: Piemonte, Veneto, Emilia-Romagna, Toscana, Basilicata. Risulta nuovo per la Lombardia.
Piante ospiti: specie del genere *Campanula*.
Alcuni esemplari raccolti in giugno nelle staz. 2 e 6, ai margini di un sentiero a nord-ovest dei Piani di Barra e presso l'Osservatorio ornitologico.

Miarus (Miaromimus) micros (Germar)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Piemonte, Veneto, Emilia-Romagna, Sicilia. La specie risulta nuova per la Lombardia.

Piante ospiti: verosimilmente Campanulacee.
Un unico reperto (staz. 6, 23.V.1991, lg. Bonini).

Miarus (s.str.) campanulae (Linneo)
Corotipo: Paleartico (PAL).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Toscana, Lazio, Campania, Calabria.
Piante ospiti: svariate Campanulacee.
Numerosi esemplari raccolti in aprile e maggio nelle staz. 2, 5, 6 e 8, presso la vetta e ai margini di un sentiero che dall'eremo porta alla Sella della Pila.

Gymnetron (s.str.) pascuorum (Gyllenhal)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia.
Piante ospiti: *Plantago lanceolata.*
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2, 5, 7, 9, presso la stazione di osservazione ornitologica e nei boschi della Val Faè.

Gymnetron (Rhinusa) tetrum (Linneo)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Verbscum*, più di rado *Scrophularia.*
Alcuni esemplari raccolti in giugno nelle staz. 3 e 9.

Gymnetron (Rhinusa) antirrhini (Paykull)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie del genere *Linaria.*
Un reperto in staz. 2 e uno in staz,5 (23.V.1991, lg. Bonini).

Gymnetron (Rhinusa) linariae (Panzer)
Corotipo: Europeo (EUR).
Presenza in Italia: noto di gran parte d'Italia settentrionale e centrale, Campania, Sicilia.
Piante ospiti: specie del genere *Linaria.*
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2 e 5 e ai margini di un sentiero a nord-ovest dei Piani di Barra.

Cionus tuberculosus (Scopoli)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia.
Piante ospiti: specie del genere *Scrophularia.*
Alcuni esemplari raccolti in maggio e giugno nelle staz. 1, 2 e ai margini di un sentiero a nord-ovest dei Piani di Barra.

Cionus olivieri Rosenschöld
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Verbascum*, soprattutto *V. thapsus.*
Alcuni esemplari raccolti in maggio e giugno nelle staz. 4 e 5.

Cionus thapsus (Fabricius)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Piante ospiti: specie del genere *Verbascum.*
Tre esemplari raccolti nella staz. 3 (18.V.1991, lg. Sassi).

Stereonychus fraxini (Degeer) s.str.
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: noto di gran parte d'Italia, Sicilia.
Piante ospiti: *Fraxinus excelsior.*
Alcuni esemplari raccolti a maggio nelle staz. 6, 7 e nei boschi della Val Faè.

Nella seguente tabella (Tabella 1) sono riuniti i dati relativi alla presenza delle specie nelle diverse stazioni. Nel numero 10 sono riunite le località del Monte Barro collocate al difuori delle stazioni di raccolta identificate con precisione; si tratta per lo più di località site nei boschi della Val Faè; indicazioni più dettagliate, peraltro, si possono ricavare dalla precedente trattazione delle singole specie.

Tabella 1 - Tabella riassuntiva delle specie raccolte.

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Lasiorhynchites sericeus										+
Coenorhinus nanus		+				+				
Coenorhinus tomentosus		+		+	+	+				
Coenorhinus germanicus	+	+	+		+	+				+
Coenorhinus aeneovirens			+							+
Coenorhinus aequatus										+
Rhynchites aethiops			+	+	+	+				+
Apoderus coryli	+	+		+	+	+				+
Attelabus nitens		+								+
Nanophyes annulatus									+	
Nanophyes marmoratus									+	
Apion armatum		+		+	+		+			+
Apion onopordi	+	+	+	+	+			+	+	+
Apion confluens			+							
Apion aeneum	+	+	+							
Apion atomarium			+	+	+					
Apion flavimanum			+							
Apion minutissimum		+	+							+
Apion oblivium			+							
Apion urticarium			+	+					+	
Apion rufirostre							+			
Apion holosericeum			+							
Apion difficile	+	+			+	+				+
Apion formaneki		+	+	+	+	+				+
Apion filirostre	+						+			
Apion nigritarse							+			
Apion fulvipes	+	+	+	+	+	+	+		+	+
Apion trifolii	+	+	+	+	+	+	+	+	+	+
Apion interjectum		+	+							
Apion apricans	+	+	+	+	+	+	+	+		+
Apion ononicola		+				+				+
Apion assimile	+	+	+	+	+	+	+	+	+	+
Apion difforme		+					+			+
Apion varipes	+		+		+	+				
Apion simum		+			+					
Apion curtirostre	+	+		+	+					+
Apion violaceum	+	+		+	+					+
Apion aciculare	+	+			+					+
Apion cruentatum		+	+	+	+		+	+		+
Apion seniculus	+	+	+	+	+	+	+	+	+	+
Apion simile		+		+	+					
Apion tenue				+			+	+		+
Apion aeneomicans						+				

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Apion loti	+	+	+	+	+	+	+			+
Apion virens	+		+	+			+	+		+
Apion ebeninum							+			
Apion pisi	+	+		+	+		+		+	+
Apion pavidum		+	+	+			+	+		+
Apion gyllenhali		+								
Apion cerdo						+				
Apion subulatum					+					
Apion opeticum						+				
Apion gribodoi										+
Apion ervi	+	+	+			+	+	+		+
Apion viciae		+	+			+	+			+
Otiorhynchus salicicola			+	+			+	+		+
Otiothynchus frescati									+	+
Otiorhynchus vehemens		+	+			+	+	+		+
Otiorhynchus carmagnolae		+			+					+
Otiorhynchus ovatus				+						
Homorhythmus hirticornis	+	+			+	+	+			+
Phyllobius subdentatus roboretanus		+	+		+	+			+	+
Phyllobius chloropus	+					+	+			+
Phyllobius virideaeris padanus	+	+	+		+					
Phyllobius pyri	+	+	+		+	+	+	+	+	+
Phyllobius etruscus			+							+
Phyllobius argentatus		+	+							+
Polydrusus marginatus										+
Polydrusus atomarius							+			
Polydrusus corruscus							+			
Polydrusus pterygomalis										+
Polydrusus cervinus		+	+	+	+	+				+
Polydrusus confluens	+		+		+					
Polydrusus sericeus		+	+	+	+	+	+		+	+
Liophloeus tessulatus					+			+		
Stasiodis parvulus	+	+	+	+	+	+		+		+
Sciaphilus asperatus										+
Strophosoma melanogrammum	+	+			+					+
Barynotus obscurus		+				+				
Sitona tibialis					+	+				+
Sitona suturalis					+					
Sitona sulcifrons argutulus	+	+	+	+	+	+	+	+	+	+
Sitona flavescens					+				+	
Sitona puncticollis	+	+								
Sitona humeralis				+	+		+		+	+
Sitona hispidulus	+		+				+	+		+
Pseudocleonus cinereus										+
Pseudocleonus grammicus		+	+							
Lixus bardanae	+									
Larinus sturnus		+	+						+	
Larinus obtusus	+	+	+		+	+				+
Hypera zoilus		+	+							+
Hypera vidua		+			+					
Hypera nigrirostris							+			
Hypera postica							+			+
Hypera venusta					+					
Donus oxalidis		+					+			+
Donus intermedius	+	+		+						
Limobius borealis	+	+		+	+	+				
Lepyrus capucinus									+	
Hylobius transversovittatus									+	
Liparus dirus		+			+	+	+			+

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Leiosoma concinnum								+		
Magdalis cerasi								+	+	+
Magdalis exarata						+				+
Acalles lemur										+
Echinodera hypocrita								+		
Mononychus punctumalbum						+			+	
Rhinoncus bruchoides	+	+		+						
Rhinoncus pericarpius	+	+		+	+				+	
Rhinoncus perpendicularis									+	
Pelenomus comari									+	
Tapinotus sellatus									+	
Ceutorhynchus floralis	+	+	+	+	+					
Ceutorhynchus erysimi	+	+	+	+						+
Ceutorhynchus contractus			+	+	+		+	+		
Ceutorhynchus cochleariae			+							
Ceutorhynchus punctiger	+	+	+					+		
Ceutorhynchus distinctus	+	+	+		+					
Nedyus quadrimaculatus		+	+		+				+	+
Thamiocolus signatus		+								
Trichosirocalus rufulus								+		
Trichosirocalus troglodytes			+		+			+		
Micrelus ericae					+					
Zacladus geranii	+	+		+	+	+	+	+	+	+
Coeliodes dryados		+								
Orobitis cyaneus										+
Baris scolopacea				+	+					
Limnobaris t-album									+	
Anthonomus rubi	+	+	+	+	+	+		+	+	+
Curculio glandium		+			+					
Curculio nucum		+			+					
Balanobius pyrrhoceras		+			+	+				+
Tychius meliloti									+	
Tychius polylineatus					+					
Tychius schneideri					+	+				
Tychius junceus						+				
Tychius stephensi	+	+	+	+	+	+		+	+	+
Tychius longicollis		+								+
Tychius picirostris			+		+					
Tychius cuprifer	+	+	+		+					+
Sibinia viscariae	+	+	+	+			+			
Sibinia pellucens		+	+	+	+					+
Dorytomus taeniatus	+									
Dorytomus rufatus									+	
Notaris scirpi									+	
Pachytychius sparsutus					+	+				+
Rhynchaenus rufus										+
Rhynchaenus signifer		+								+
Rhynchaenus salicis									+	
Rhamphus pulicarius										+
Mecinus janthinus		+			+				+	
Mecinus pyraster			+	+	+				+	+
Mecinus circulatus	+								+	+
Miarus graminis		+			+	+		+	+	+
Miarus distinctus		+				+				+
Miarus micros						+				
Miarus campanulae		+			+	+		+		+
Gymnetron pascuorum	+	+			+		+		+	+
Gymnetron tetrum			+						+	
Gymnetron antirrhini		+			+					

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Gymnetron linariae	+	+			+					+
Cionus tuberculosus	+	+								+
Cionus olivieri				+	+					
Cionus thapsus			+							
Stereonychus fraxini						+	+			+

Considerazioni conclusive

Col presente lavoro vengono segnalate 166 specie di Curculionidae (sensu lato) per la zona del M. Barro. Come già accennato in apertura, si tratta di un quadro sufficientemente ampio della fauna dell'area in questione, anche se mancano alcuni elementi, sicuramente presenti, il cui campionamento avrebbe richiesto tecniche di raccolta mirate, come ad esempio le specie della tribù Cossonini, gli *Acalles* e più generalmente le specie strettamente legate al terreno. Gli elementi raccolti, peraltro, consentono di delineare un quadro sicuramente significativo della fauna curculioniodica, dal quale emerge una prevalenza di specie mesoterme ad ampia distribuzione, come si può rilevare dalla tabella 2, basata sulle categorie corologiche delle specie censite e dalla fig. 7, dove i corotipi sono raggruppati per categorie sintetiche.

Tabella 2 - Spettro corologico delle specie raccolte. Le sigle dei corotipi fondamentali sono ricavate dal lavoro di Vigna Taglianti et al. (1991).

Corotipo	n° specie	% sul totale
Europeo (EUR)	49	29,52
Paleartico (PAL)	32	19,28
Sibirico-europeo (SIE)	20	12,05
Europeo-mediterraneo (EUM)	19	11,45
W-paleartico (WPA)	9	5,42
Centroeuropeo (CEU)	8	4,82
Centroasiatico-europeo (CAE)	7	4,22
Alpino	6	3,61
Asiatico-europeo (ASE)	4	2,41
Sudeuropeo (SEU)	4	2,41
Alpino-appenninico	3	1,81
Mediterraneo (MED)	2	1,20
W-mediterraneo (WME)	1	0,60
W-europeo (WEU)	1	0,60
Olartico (OLA)	1	0,60
TOTALE	166	100,00

Per quanto riguarda il confronto fra le stazioni 1-9 in base alle specie che vi sono presenti, utilizzando l'indice di Dice/Sorensen e applicando la cluster analysis secondo il metodo WPGMA si è ottenuto il dendrogramma di somiglianza riportato in fig. 8. Prescindendo dalla contrapposizione fra la stazione 9 e le rimanenti, abbastanza ovvia in considerazione delle caratteristiche particolari di quel biotopo, si separano in primo luogo i due prati della Val Faè, probabilmente per via della loro esposizione fresca, e successivamente la stazione 6, che, oltre ad essere la più xerotermica, si distingue fisionomicamente dalle altre stazioni prative per la tendenza molto più spiccata alla ricostruzione della foresta.

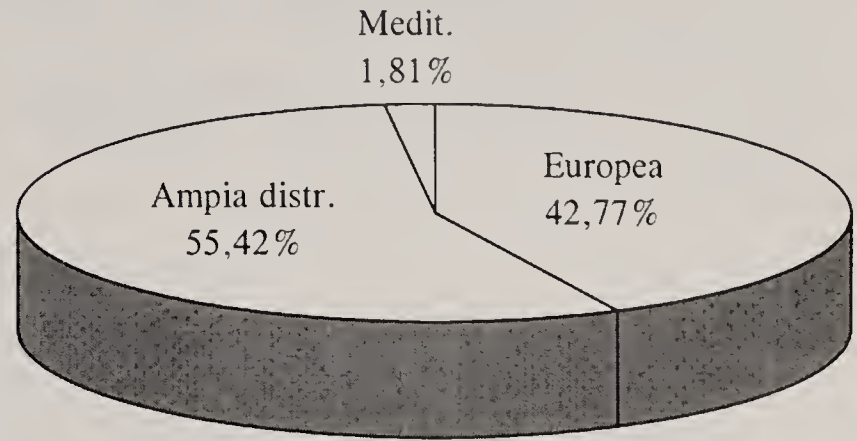



Fig. 7 - Corotipi raggruppati per categorie sintetiche.

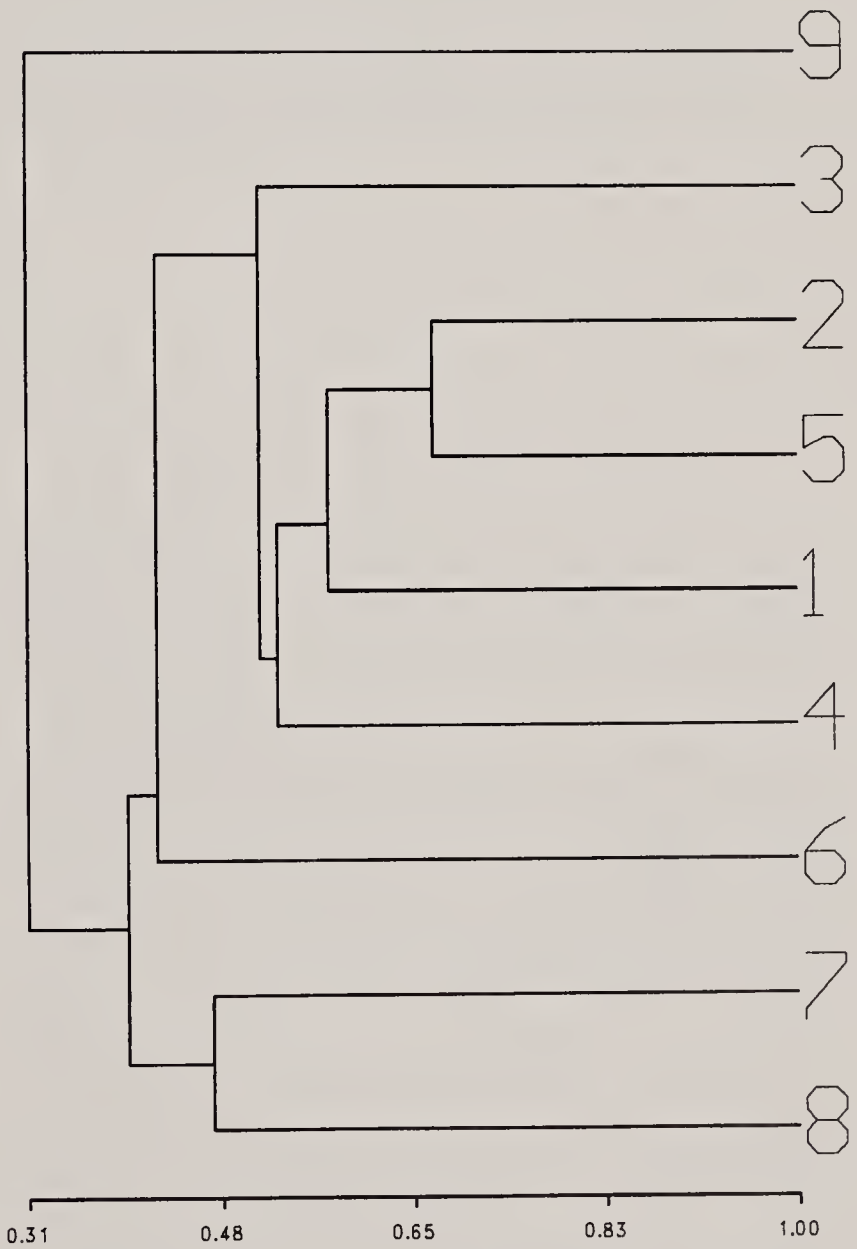



Fig. 8 - Dendrogramma di similarità fra le stazioni 1-9 basato sui campionamenti di Curculionidi (indice di Dice/Sorensen + WPGMA).

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Fausto Pesarini

Gli Imenotteri Sinfiti (Hymenoptera Megalodontidae, Cephidae, Argidae, Cimbicidae, Tenthredinidae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - L'autore presenta un elenco di 43 specie di Imenotteri Sinfiti censite nell'area del Monte Barro (Lecco). Il materiale è stato raccolto nell'ambito di una ricerca entomofaunistica condotta dal Museo di Storia Naturale di Milano negli anni 1989-1992. La maggior parte delle raccolte è stata effettuata in nove stazioni prative (staz. 1-9), 8 delle quali situate all'interno del parco regionale. Di ciascuna stazione è fornita una breve descrizione. Per ognuna delle specie censite si forniscono i dati corologici e biologici essenziali e il numero di esemplari raccolti in ogni stazione con l'indicazione del sesso. Due specie (*Tenthredo diana e Macrophya rufipes*) sono risultate nuove per la Lombardia.

Abstract - Sawflies (Hymenoptera Megalodontidae, Cephidae, Argidae, Cimbicidae, Tenthredinidae) from Monte Barro (Italy, Lombardy, Lecco).

The author makes a list of 43 species of Hymenoptera Symphyta collected in the area of Monte Barro (Lecco). The material has been sampled during a research accomplished by the Natural History Museum of Milano in the years 1989-1992. Nine sampling sites (eight of which placed inside the Regional Park) have been especially investigated and briefly described. For each sampled species biological and distributional data are given, together with the number of both male (m) and female (f) collected specimens. Two species (*Tenthredo diana and Macrophya rufipes*) are new for Lombardy.

Key words: Monte Barro, Symphyta, geographical distribution.

Nel corso delle campagne di raccolta sulla entomofauna del Monte Barro, condotte dal Museo Civico di Storia Naturale di Milano negli anni 1989-1992, sono stati campionati 136 esemplari di Imenotteri Sinfiti appartenenti a 43 specie. Si tratta di un piccolo contingente, che potrebbe certamente venire molto incrementato con ulteriori indagini. Pur con evidenti lacune (quali ad esempio l'unica specie, per di più alquanto banale, di Nematinae), si può però considerare tale campione discretamente indicativo della fisionomia dell'ambiente indagato e della sinfitofauna relativa. È degna di nota, infatti, la notevole aliquota di specie infeudate a poacee (almeno 13 su 43, pari al 30,2 %), molte volte superiore all'analoga quota (4,2 %) che si ottiene prendendo in esame l'intero complesso di specie europee di Sinfiti di cui è nota le pianta ospite (Liston, 1995). Pur non potendo escludere che abbiano avuto un'influenza non trascurabile, nella composizione del campione, le tecniche di raccolta impiegate, nonché la stessa casualità (visto il numero complessivamente modesto di specie censite), sembra però plausibile ricollegare tale dato ad elementi fisionomici propri delle biocenosi oggetto di studio.

Nel complesso delle specie censite, due sono risultate nuove per la Lombardia (*Tenthredo diana* Benson e *Macrophya rufipes* (L.)), mentre altre tre (*Sterictiphora angelicae* (Panzer), *Tenthredopsis dubia* Konow e *Tenthredopsis palmata* (Geoffroy)) erano state segnalate, per la stessa regione, sotto altro nome.

Osservazioni sulle stazioni di raccolta

La maggior parte delle raccolte va riferita a 9 stazioni prative (staz. 1-9) di cui si riportano le caratteristiche ambientali ricavate dal contributo di Banfi, Galasso & Sassi, in questo stesso volume. Altre stazioni sono state riunite, nella tabella riassuntiva (tab. 1), sotto il numero 10.

Stazione 1: Località Piani di Barra, 610 m, esp. W, interessata da scavi archeologici (Grande Edificio). È caratterizzata da una consistente presenza di prato falciabile che indica una attività di foraggio residua.

Stazione 2: Località Piani di Barra, 600 m, esp. W, interessata da scavi archeologici (Edificio II). Si tratta di una prateria in cui è stata abbandonata la gestione a foraggio, vi è quindi presente un leggero mantello.

Stazione 3: Conca prativa a monte del Monumento dell'Alpino, 630 m, esp. W. Vi si nota la convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion* è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. È un prato arido con montarozzi residui a brughiera; per il resto il livello di base è costituito da prateria a *Brachypodium rupestre* ssp. *caespitosum*.

Stazione 6: Superfici prative lungo il sentiero della «Cresta occidentale», che dall'edificio dell'ex sana-

torio sale alla vetta, 750 m, esp. S. Si tratta di una prateria con parziale affioramento roccioso, fortemente cespugliata e in via di chiusura, con forte influsso dell'elemento prenemorale (tendenza a un *Quercetum pubescentis* s. l.)

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. È una superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8 ma più aperta e con qualche elemento in più di *Mesobromion*.

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. È un prato terrazzato irregolarmente gestito e contornato da un bosco con notevoli contrassegni mesofili.

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Vi si evidenziano tre aspetti essenziali: 1) il canneto, con accenni di aggruppamento a *Iris pseudoacorus*, elementi di magnocariceto e residui di boscaglia ripariale 2) prato umido oligotrofico (*Molinion coeruleae*); 3) vegetazione erbacea perenne e disorganizzata al margine superiore della stazione.

Elenco delle specie raccolte

Nell'elenco che segue si è adottato l'ordinamento seguito nella recentissima check-list dei Sinfiti italiani di Masutti & Pesarini (1995).

Megalodontidae
Megalodontes cephalotes (Fabricius, 1781)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni settentrionali, Toscana.
Piante ospiti: Apiacee del genere *Peucedanum*.
Staz.4: 10.VI.91, leg. Leonardi, 1 f; 18.VI.91, leg. Sassi, 1 f. Staz. 5: 10.VI.90, leg. Sassi, 1 f. Staz. 7: 19.V.92, leg. Sassi, 1 f.

Megalodontes klugii (Leach, 1817)
= *M. spissicornis* (Klug, 1824)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni settentrionali, Toscana.
Piante ospiti: Apiacee dei generi *Laserpitium, Peucedanum, Seseli*.
1 f, 30.V.90, leg. Sassi, sul versante meridionale, ai margini di un sentiero che va dall'eremo alla Sella della Pila.

Cephidae
Cephus brachycercus Thomson, 1871
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni settentrionali, Toscana, Marche, Lazio, Sardegna.
Piante ospitl: sconosciute, con molta probabilità poacee.
Staz. 1: 23.V.91, leg. Sassi, 1 f. Staz. 2: 23.V.91, leg. Leonardi, 1 f. Staz. 4, 23.V.91, leg. Leonardi, 3 ff.

Cephus cultratus Eversmann, 1847
= *C. pilosulus* Thomson, 1871
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, Toscana e Sicilia.
Piante ospiti: Poacee dei generi *Phleum* e *Dactylis*.
Staz. 1: 23.V.91, leg. Sassi, 1 m; 30.V.9l, leg. Sassi, 1 m. Staz. 2: 10.VI.91. leg. Leonardi, 1 f. Staz. 3: 30.V.91, leg. Leonardi, 1 f.

Calameuta pallipes (Klug, 1803)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Valle d'Aosta, Lombardia, Liguria, Calabria, Sardegna.
Piante ospiti: sconosciute, con molta probabilità poacee.
Staz. 1: 30.V.91, leg. Leonardi, 1 f. Staz. 2: 15.VI.89, leg. Leonardi, 1 f; 10.VI.91, leg. Leonardi, 1 m. Staz. 8: 19.V.92, leg. Sassi, 1 f.

Argidae
Sterictiphora angelic**ae** (Panzer, 1799)
= *S. furcata* auctt., partim, nec Villers, 1789
Corotipo: Europeo (EUR).
Presenza in Italia: a lungo confusa con *S. furcata* (Villers), l'unico dato Pubblicato era relativo all'Appennino Romagnolo (Pesarini & Campadelli, in stampa). Ne ho potuti esaminare, in realtà, esemplari provenienti da svariate regioni, ed è probabile che molti dei reperti di *S. furcata* della letteratura siano da assegnare a *S. angelicae*. Di Lombardia essa mi è nota anche di Caslino al Piano (Pesarini, 1983, sub *S. furcata*) e di Mercallo (in coll. Museo di Milano).
Piante ospiti: sconosciute, probabilmente rosacee.
Staz. 1: 19.V.91, leg. Leonardi, 1 m.

Cimbicidae
Corynis obscura (Fabricius, 1775)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia e Sicilia.
Piante ospiti: probabilmente *Geranium sylvaticum*.
Staz. 6: 27.VI.89, leg. Leonardi, 1 f 1 m.

Tentredinidae
Selandriinae
Brachytops flavens (Klug, 1814)
Corotipo: Olartico (OLA).
Presenza in Italia: nonostante l'enorme areale, per il nostro Paese risulta segnalato solo di Piemonte, Lombardia e Veneto.
Piante ospiti: Ciperacee del genere *Carex*.
Staz. 2: 9.IV.90, leg. Leonardi, 1 f 3 mm. Staz. 9: 15.VI.90, leg. Leonardi, 1 m.

Dolerus (Dicrodolerus) vestigialis (Klug, 1814)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni settentrionali e peninsulari.
Piante ospiti: *Equisetum palustre* e *sylvaticum*.
Staz. 9: 19.V.91, leg. Leonardi, 1 f.

Dolerus (Poodolerus) gonager (Fabricius, 1781)
Corotipo: S1birico-Europeo (SIE).
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Calabria.
Piante ospiti: Poacee dei generi *Agrostis*, *Festuca*, *Poa*.
Staz. 3: 19.V.91, leg. Leonardi, 1 f. Staz. 4: 30.III.90, leg. Leonardi, 1 f; 23.V.91, leg. Leonardi, 1 f.

Dolerus (Poodolerus) niger (Linnaeus, 1767)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Campania e Calabria.

Piante ospiti: poacee dei generi *Avena, Hordeum. Triticum.*
Staz. 1: 23.V.91, leg. Sassi, 1 f.

Dolerus (Poodolerus) picipes (Klug. 1814)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, Marche, Calabria.
Piante ospiti: Poacee dei generi *Agrostis* e *Festuca.*
Staz. 4: 23.V.91, leg. Leonardi, 1 f; 30.V.91, leg. Leonardi, 1 f. Staz. 5: 30.V.91, leg. Leonardi, 1 f.

Dolerus (Poodolerus) puncticollis Thomson, 1871
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, Toscana, Calabria; mi è noto anche di Lazio, Abruzzo e Puglia (Gargano).
Piante ospiti: sconosciute, con tutta probabilità poacee.
Staz. 8: 14.III.90, leg. Sassi, 1 f.

Tenthredininae
Aglaostigma aucupariae Klug, 1814)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Basilicata.
Piante ospiti: *Galium mollugo* e *boreale.*
Staz. 2: 19.V.91, leg. Leonardi, 1 m. Staz. 7: 21.IV.92, leg. Sassi, 1 f.

Aglaostigma fulvipes (Scopoli, 1763)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Trentino, Friuli, Emilia-Romagna e Toscana; mi è noto anche di Piemonte, Veneto, Liguria, Marche, Abruzzo e Calabria.
Piante ospiti: *Galium.*
Staz. 4: 30.III.90, leg. Sassi, 1 f.

Tenthredopsis dubia Konow, 1890
= *T. picticeps* auctt. nec Cameron, 1881
Corotipo: Europeo (EUR).
Presenza in Italia: da precisare, data l'estrema incertezza sull'identità delle specie del genere *Tenthredopsis* Costa. Con i nomi di *T. dubia* Konow o *picticeps* Cameron risulta segnalata di Veneto, Emilia-Romagna e Abruzzo, ma è certamente molto più diffusa. Di Lombardia mi era nota di Faloppio, Olgelasca, Capriano, Calolziocorte (Pesarini, 1983, sub *T. nassata* (L.), partim).
Piante ospiti: *Triticum vulgare* e *Agropyron repens.*
Staz. 1: 19.V.91, leg. Leonardi, 1 f. Staz. 2: 23.V.91, leg. Leonardi, 1 m. Staz. 6: 19.V.92, leg. Sassi, 1 f. Staz. 7: 21.IV.92, leg. Leonardi, 1 m.

Tenthredopsis nassata (Linnaeus, 1767)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: tutta Italia continentale, forse Sicilia.
Piante ospiti: Poacee dei generi *Agropyron* e *Deschampsia*; anche *Carex.*
Staz. 6: 19.V.92, leg. Sassi, 2 mm. Staz. 7: 19.V.92. leg. Sassi, 1 f.

Tenthredopsis palmata (Geoffroy, 1785)
= *T. campestris* auctt., Partim, nec Linnaeus, 1758
= *T. scutellaris* (Fabricius, 1798)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: da precisare, per le stesse ragioni esposte al riguardo di *T. dubia* Konow; sembra comunque essere meno diffusa e frequente di quest'ultima. Di Lombardia mi era nota di Olgiate Comasco, Caslino al Piano, Verano Brianza, Sartirana, Brivio (Pesarini, 1983, sub *T. nassata* (L.), partim).
Piante ospiti: Poacee dei generi *Agropyron, Dactylis, Festuca* e *Poa.*
Staz. 2: 23.V.91, leg. Sassi, 1 f. Staz. 6, 19.V.92, leg. Sassi. 1 m; Boschi della Val Faè, 19.V.92, leg. Sassi, 1 f.

Tenthredopsis sordida (Klug, 1814)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: regioni settentrionali, Toscana, Abruzzo, Campania, Basilicata, Calabria.
Piante ospiti: Poacee dei generi *Agropyron. Arrhenaterum, Lolium*; anche *Carex.*
Staz. 1: 19.V.91, leg. Leonardi, 1 f. Staz. 2: 9.V.90, leg. Sassi, 1 f 2 mm; 23.V.91, leg. Leonardi, 1 f; 30.V.91, leg. Leonardi, 1 f. Staz. 8, 16.V.90, 1 f. Inoltre 2 mm (25.IV.90, leg. Sassi) in un prato della val Faè prossimo alla staz. 7.

Tenthredopsis stigma (Fabricius, 1798)
Corotipo: Europeo (EUR).
Presenza in Italia: regioni settentrionali, Toscana, Abruzzo, Campania, Calabria.
Piante ospiti: *Triticum intermedium.*
Staz. 6: 19.V.92, leg. Sassi, 2 ff 2 mm. Staz. 8: 19.V.92, leg. Sassi, 1 f.

Rhogogaster genistae Benson, 1949
Corotioo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Piemonte, Lombardia, Friuli-Venezia Giulia, Liguria, Emilia-Romagna, Toscana.
Piante ospiti: *Sarothamnus* e *Genista.*
Staz. 5: 30.V.91, leg. Sassi, 1 m.

Rhogogaster viridis (Linnaeus, 1758)
Corotipo: Olartico (OLA).
Presenza in Italia: in Passato venivano confuse con *Rh. viridis* (L.) almeno altre due specie del genere *Rhogogaster* Konow. I dati certi riguardano le regioni settentrionali, la Toscana e il Lazio.
Piante ospiti: specie spiccatamente polifaga, si sviluppa su *Salix. Populus, Quercus.* e più tipicamente *Alnus*; ma anche su *Stellaria, Filipendula, Circaea, Epilobium* (*Chamnaerion*).
Staz. 5: 16.V.90, leg. Sassi, 1 f. Staz. 6: 19.V.92, leg. Sassi, 1 f.

Tenthredo brevicornis Konow, 1886)
= *T. nitidior* Konow, 1888 = *acerrima* Benson, 1952
Corotipo: Europeo (EUR).
Presenza in Italia: per lungo tempo confusa con almeno tre altre specie del gruppo *arcuata*; i dati certi riguardano le regioni settentrionali (Alpi e pedemonte alpino) e l'Appennino dall'Emilia al Molise.
Piante ospiti: *Lotus corniculatus.*
Staz. 1: 18.VI.91, leg. Sassi, 1 m; 10.X.91, leg. Sassi, 3 ff. Staz. 2: 9.V.90. leg. Sassi, 1 f.

Tenthredo notha Klug, 1814
= *T. perkinsi* Morice, 1919
Corotipo: Europeo (EUR).
Presenza in Italia: valgono le considerazioni fatte per la precedente specie. I dati certi riguardano l'in-

tero arco alpino. l'Abruzzo (Gran Sasso) e il Molise (Matese).
Piante ospiti: *Trifolium repens*, *Vicia cracca*.
Boschi della Val Faè, 13.1X.90, leg Leonardi, 1 f.

Tenthredo sp. gruppo ***arcuata***
Staz. 4: 10.VI.91, leg. Leonardi. 1 m.

Tenthredo diana Benson, 1968
Corotipo: Europeo (EUR).
Presenza in Italia: descritta come sottospecie appenninica di *T. maculata* Geoffroy, *T. diana* è stata riconosciuta come specie distinta solo di recente (Pesarini, 1989) ed è in realtà assai più ampiamente diffusa di quanto non si ritenesse un tempo; è attualmente nota di Italia e di Francia, il suo areale di distribuzione resta però da precisare, perchè è probabile sia stata per molto tempo confusa con la specie affine. In Italia i dati certi riguardano Piemonte, Emilia-Romagna, Toscana, Marche, Abruzzo; nuova per la Lombardia.
Piante ospiti: sconosciute; l'affine *T maculata* si sviluppa su Poacee dei generi *Brachypodium* e *Dactylis*.
Staz. 6: 19.V, 92, leg. Sassi, 2 ff.

Pachyprotasis rapae (Linnaeus, 1767)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni settentrionali e peninsulari.
Piante ospiti: specie polifaga; si sviluppa principalmente su varie Lamiacee, Scrofulariacee, Solanacee e Asteracee, ma anche su *Plantago*, *Hypericum*, *Epilobium*, *Angelica*, *Sarothamnus*, *Fraxinus*, *Quercus*, *Corylus*.
Boschi della Val Faè, 13.IX.90, leg. Sassi, 1 f. Prato adiacente alla staz. 4, 13.IX.90, leg. Sassi, 1 f.

Macrophya albipuncta (Fallén, 1808)
Corotipo: Europeo (EUR).
Presenza in Italia: Lombardia, Emilia-Romagna, Toscana; probabilmente è molto più diffusa, ma non è frequente.
Piante ospiti: *Geranium sylvaticum*.
Staz. 1: 30.V.91, leg. Sassi, 1 m. Staz. 2, 23.V.91, leg. Leonardi, 1 f; idem, leg. Sassi, 1 f 1 m; 9.VI.91, leg. Sassi. 1 f. Staz. 6, 19.V.92. leg. Sassi. 1 m.

Macrophya annulata (Geoffroy, 1785)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutte le regioni settentrionali e peninsulari, Sicilia.
Piante ospiti: in letteratura è riportata più frequentemente *Potentilla reptans*, ma sono indicati anche *Rosa*, *Rubus* e *Origanum*.
Staz. 2: 15.VI.89, leg. Leonardi, 3 ff; 9.VI.91, leg. Sassi, 1 m; 10.VI.91, leg. Leonardi, 2 ff 1 m; 18.VI.91, leg. Sassi, 2 ff 1 m. Staz. 4: 10.VI.91, leg. Leonardi, 1 f. Staz. 5: 30.V.91, leg. Sassi. 1 f; 18.VI.91, leg. Sassi, 1 f. Tornante lungo la strada che sale al monumento dell'Alpino, 9.VI.91, leg. Sassi, 1 f.

Macrophya duodecimpunctata (Linnaeus, 1758)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Abruzzo, Campania, Basilicata, Calabria.
Piante ospiti: Poacee a foglia coriacea e Ciperacee (*Carex*).
Staz. 2: 18.VI.91, leg. Sassi, 1 m. Staz. 9: 16.V.90, leg. Leonardi. 2 mm; idem, leg. Sassi, 2 ff 2 mm; 15.VI.91, leg. Leonardi, 1 f.

Macrophya rufipes (Linnaeus, 1758)
Corotipo: Turanico-Europeo (TUE).
Presenza in Italia: Piemonte, Emilia-Romagna, Toscana, Abruzzo. Sicilia. Probabilmente presente in tutta Italia come già riportava genericamente Costa (1894); in letteratura non esistevano comunque dati lombardi. Di questa regione mi è nota anche del Lago d'Endine (in Coll. Pesarini).
Piante ospiti: non note con certezza; forse *Vitis vinifera*.
Staz. 9: 15.VI.90, leg. Leonardi, 1 f.

Allantinae
Empria tridens (Konow, 1896)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: da precisare; i dati di letteratura riguardano Piemonte e Lombardia.
Piante ospiti: Rosacee dei generi *Rubus* e *Geum*.
Boschi della Val Faè, 25.VI.90, leg. Sassi, 1 f.

Ametastegia tenera (Fallén, 1808)
Corotipo: Olartico (OLA).
Presenza in Italia: Piemonte, Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Liguria; genericamente indicata di Sicilia.
Piante ospiti: piante erbacee varie: *Cyrsium lanceolatum*, *Filipendula ulmaria*, più tipicamente *Rumex* spp..
Staz. 3: 14.III.90, leg. Leonardi, 1 f. Staz. 4: 26.IX.92, leg. Leonardi, 1 f. Boschi della Val Faè, 25.VI.90, leg. Sassi, 1 m.

Emphytus calceatus (Klug, 1814)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Abruzzo; citato di Sardegna, ma il dato probabilmente è da riferire a *E. laticinctus* (Lepeletier, 1823) (= *E. balteatus* (Klug, 1818 nec Klug, 1817)).
Piante ospiti: Rosacee di svariati generi: *Filipendula, Fragaria, Rosa, Rubus, Alchemilla, Sanguisorba.*
Staz. 9: 15.VI.90, leg. Leonardi, 1 f; 16.V.91, leg. Sassi, 1 f; 19.V.91, leg. Leonardi, 1 f.

Emphytus cingulatus (Scopoli, 1763)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Marche, Abruzzo, Campania. Calabria, Sicilia, Sardegna.
Piante ospiti: *Fragaria* e *Rosa*, ma anche *Corylus* e *Betula*.
Staz. 2: 15.VI.89. leg. Leonardi, 1 f.

Athaliinae
Athalia circularis (Klug, 1813)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali e peninsulari, Sardegna.
Piante ospiti: varie Lamiacee e Scrofulariacee, ma anche *Plantago* e *Capsella*.
Staz. 9: 25.V.90, leg. Sassi, 1 m.

Athalia cordata Lepeletier, 1823
Corotipo: W-Paleartico (WPA).

Presenza in Italia: regioni settentrionali e peninsulari, Sardegna.
Piante ospiti: piante erbacee varie: *Ajuga, Antirrhinum* e *Plantago*.
Staz. 3: 13.IX.90, leg. Leonardi, 1 f. Staz. 4, 26.IX.92, leg. Leonardi, 1 f. Staz. 7: 21.IV.92. leg. Sassi, 1 f. Prato adiacente alla staz. 4, 13.IX.90, leg. Sassi, 1 f.

Athalia glabricollis Thomson, 1870
Corotipo: W-paleartico (WPA).
Presenza in Italia: tutta Italia, incluse Sicilia e Sardegna.
Piante ospiti: Brassicacee dei generi *Diplotaxis, Erysimum, Raphanus, Sinapis* e *Sisymbrium*.
Staz. 4: 20.IX.89, leg. Leonardi. 1 f.

Blennocampinae
Monophadnus pallescens (Gmelin. 1790)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni settentrionali, Toscana, Basilicata, Calabria.
Piante ospiti: diverse specie del genere *Ranunculus*.
Staz. 3: 14.III.90, leg. Leonardi, 1 f; idem, leg. Sassi, 1 f. Staz. 4: 30.III.90, leg. Sassi, 1 f. Staz. 8, 14.III.90, leg. Leonardi, 2 ff 2 mm; idem. leg. Sassi, 5 ff 1 m.

Stethomostus fuliginosus (Schrank, 1781)
Corotipo: Asiatico-Europeo (ASE); introdotto in Nord America.
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Abruzzo, Campania, Calabria.
Piante ospiti: diverse specie del genere *Ranunculus*.
Staz. 9: 15.VI.90, leg. Leonardi, 1 m.

Eutomostethus luteiventris (Klug, 1814)
Corotipo: Europeo (EUR); introdotto in Nord America.
Presenza in Italia: regioni settentrionali, Toscana, Lazio, Calabria.
Piante ospiti: *Juncus effusus*.
Staz. 9: 15.VI.90. leg. Leonardi, 1 f.

Claremontia confusa (Konow, 1886)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: regioni settentrionali, Calabria; citata da Costa (1894) anche di Sardegna sub *Blennocampa cinereipes* (Hartig).
Piante ospiti: Rosacee dei generi *Sanguisorba, Potentilla, Fragaria*.
Staz. 9: 30.III.90, leg. Sassi, 1 f.

Nematinae
Cladius pectinicornis (Geoffroy, 1785)
Corotipo: Olartico (OLA).
Presenza in Italia: regioni settentrionali, Toscana, Sardegna; probabilmente diffuso in tutto il Paese, ma i molti dati esistenti in letteratura possono riferirsi all'affine *C. difformis* (Panzer, 1799).
Piante ospiti: Rosacee dei generi *Filipendula, Fragaria, Rosa, Sanguisorba*; forse *Lamiastrum galeobdolon*.
Staz. 1: 10.X.91, leg. Sassi, 1 f. Staz 9: 30.III.90, leg. Sassi, 1 f; 15.VI.90, leg. Leonardi, 1 f.

Tabella 1 - Tabella riassuntiva delle specie raccolte.

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Megalodontes cephalotes				+	+		+			
Megalodontes klugii										+
Cephus brachycercus	+	+		+						
Cephus cultratus	+	+	+							
Calameuta pallipes	+	+						+		
Sterictiphora angelicae	+									
Corynis obscura						+				
Brachytops flavens		+							+	
Dolerus vestigialis									+	
Dolerus gonager			+	+						
Dolerus niger	+									
Dolerus picipes				+	+					
Dolerus puncticollis								+		
Aglaostigma aucupariae		+					+			
Aglaostigma fulvipes				+						
Tenthredopsis dubia	+	+				+	+			
Tenthredopsis nassata						+	+			
Tenthredopsis palmata		+				+				+
Tenthredopsis sordida	+	+						+		+
Tenthredopsis stigma						+		+		
Rhogogaster genistae					+					
Rhogogaster viridis					+	+				
Tenthredo brevicornis	+	+								
Tenthredo notha										+
Tenthredo diana						+				
Tenthredo sp.				+						
Pachyprotasis rapae										+
Macrophya albipuncta	+	+				+				
Macrophya annulata		+		+	+					+
Macrophya duodecimpunctata		+							+	
Macrophya rufipes									+	
Empria tridens										+
Ametastegia tenera			+	+						+
Emphytus calceatus									+	
Emphytus cingulatus		+								
Athalia circularis									+	
Athalia cordata			+	+			+			+
Athalia glabricollis				+						
Monophadnus pallescens			+	+				+		
Stethomostus fuliginosus									+	
Eutomostethus luteiventris									+	
Claremontia confusa									+	
Cladius pectinicornis	+								+	

Considerazioni zoogeografiche

Il quadro corologico delle specie raccolte sul Monte Barro indica una netta predominanza di elementi ad ampia distribuzione paleartica e la totale assenza di specie mediterranee, come si può vedere dalla tabella 2 e, con maggior evidenza, dalla figura 1, dove i corotipi sono stati raggruppati per categorie sintetiche.

Tabella 2 - Spettro corologico delle specie raccolte. I corotipi sono stati definiti in base al lavoro di Vigna Taglianti et alii (1992).

Corotipo	n° specie	% sul totale
Europeo (EUR)	13	30,95
Sibirico-Europeo (SIE)	8	19,05
Olartico (OLA)	7	16,67
Asiatico-Europeo (ASE)	6	14,29
Centroeuropeo (CEU)	4	9,52
W-Paleartico (WPA)	2	4,76
Turanico-Europeo (TUE)	1	2,38
Europeo-Mediterraneo (EUM)	1	2,38
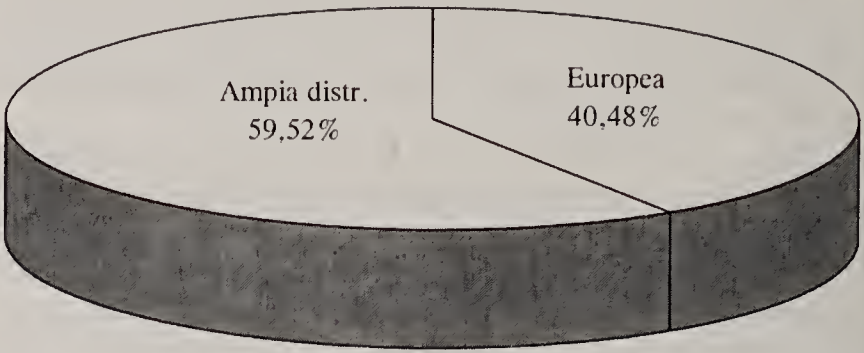
Fig. 1 - Corotipi raggruppati per categorie sintetiche.

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Fausto Pesarini: Museo Civico di Storia Naturale, Via De Pisis, 24 - 44100 Ferrara

Carlo Pesarini

I Ragni (Arachnida Araneae) del Monte Barro (Italia, Lombardia, Lecco)

Riassunto - Col presente lavoro sono forniti i dati relativi al popolamento araneologico del Monte Barro (Lecco), come risultato di una ricerca condotta negli anni 1989-1992 dal Museo di Storia Naturale di Milano col contributo del Consorzio Parco Monte Barro. Le raccolte sono state effettuate prevalentemente in 9 stazioni prative. Vengono analizzate le caratteristiche biogeografiche della popolazione araneologica, e vengono segnalate 32 specie come nuove per la fauna lombarda, fra le quali 5 (*Ceratinella scabrosa, Erigone autumnalis, Enoplognatha thoracica, Cheiracanthium montanum, Philodromus praedatus*) nuove per la fauna italiana.

Abstract - Spiders (Arachnida Araneae) from Monte Barro (Italy, Lombardy, Lecco).
In the present work data concerning the spider-fauna of the Monte Barro are given, as result of a research carried out by the Natural History Museum of Milano in the years 1989-1992. Meadows have been chiefly investigated, with particular regard to 9 sampling sites.The biogegraphic pattern of the spider-population is analyzed; furthermore, 32 species are recorded as new for the Lombard fauna, 5 among which (*Ceratinella scabrosa, Erigone autumnalis, Enoplognatha thoracica, Cheiracanthium montanum, Philodromus praedatus*) are new for Italy.

Key words: Monte Barro, Araneae, geographic distribution.

Negli anni 1989-1992 il Museo Civico di Storia Naturale di Milano ha condotto una ricerca entomofaunistica nell'area del Monte Barro (Lombardia, Lecco) col contributo del Consorzio Parco. Per quanto riguarda la fauna araneologica, alle raccolte effettuate da Davide Sassi e Carlo Leonardi sono da aggiungersi quelle prodotte, nell'ambito di un lavoro di tesi di laurea da me coordinato, dalla Dr.ssa Monica Aureggi. Il quadro complessivo così ottenuto è discretamente ricco, anche se verosimilmente non del tutto completo. Si riscontrano infatti delle lacune per quanto riguarda la fauna del terreno, sicuramente molto più abbondante di quanto non appaia dall'elenco qui fornito; ciò va imputato alla modalità delle ricerche condotte, indirizzate essenzialmente ad un monitoraggio della fauna legata alla vegetazione. A dispetto di tale lacuna, peraltro, i dati ottenuti sono di indubbio interesse, ed hanno condotto alla segnalazione di 32 specie nuove per la Lombardia, fra cui 5 nuove per la fauna italiana (*Ceratinella scabrosa, Erigone autumnalis, Enoplognatha thoracica, Cheiracanthium montanum, Philodromus praedatus*). Tale segnalazione viene fornita in modo generico per l'Italia settentrionale nella check-list delle specie italiane da me recentemente pubblicata (Pesarini, 1995); dati più dettagliati, limitatamente alle specie di Linyphiidae della sottofamiglia Erigoninae sono invece da me forniti in un'altra pubblicazione attualmente in stampa.

Osservazioni sulle stazioni di raccolta

Le raccolte sono state effettuate prevalentemente in nove stazioni (staz.1-9) caratterizzate da una forte presenza prativa; ulteriori stazioni di raccolta sono state riunite, nel quadro riassuntivo (Tabella 1), in una sorta di stazione cumulativa indicata con il numero 10.

Qui di seguito è data una breve descrizione delle stazioni 1-9; esse corrispondono più o meno a quelle della ricerca generale ma hanno quasi sempre confini più ampi e in alcuni casi sono fisionomicamente più varie. Per ogni stazione sono indicati i taxa esclusivi (specificità). Le specie contrassegnate da un *, pur essendo state rinvenute in una sola delle nove stazioni considerate, risultano presenti in uno o più dei biotopi riuniti al numero 10.

Stazione 1: Località Piani di Barra, 610 m. esp. W, interessata da scavi archeologici (Grande Edificio). È caratterizzata da una consistente presenza di prato falciabile che indica un'attività di foraggio residua.

Specificità: *Clubiona terrestris**.

Stazione 2: Località Piani di Barra, 600 m, esp. W, interessata da scavi archeologici (Edificio II). Si tratta di una prateria in cui è stata abbandonata la gestione a foraggio ed è presente un leggero mantello con forte copertura di *Geranium sanguineum*. Nella stessa area si collocano boschi moderatamente termofili con *Quercus pubescens, Ostrya carpinifolia e Corylus avellana*.

Specificità: *Aculepeira ceropegia, Porrhomma pygmaeum, Episinus truncatus*, Trochosa ruricola*, Xerolycosa nemoralis*, Xysticus bufo*, Brigittea latens, Heliophanus aeneus.*

Stazione 3: Conca prativa a monte del Monumento dell'Alpino, 630 m, esp. W. Vi si nota la convivenza di elementi di prateria, elementi di prato falciabile ed elementi di disturbo marginale.

Specificità: *Araneus sturmi, Ar. triguttatus, Meioneta rurestris, Cheiracanthium montanum.*

Stazione 4: Località S. Michele, pendio in prossimità del sentiero per Pian Sciresa, 325 m, esp. E. Su una base di *Mesobromion* è in pieno sviluppo il prato falciabile, che qui presenta il carattere oligo-mesotrofico.

Stazione 5: Località Pian Sciresa, 435 m, esp. NE. Prevalenza di prateria arida a *Brachypodium rupestre* ssp. *caespitosum*, con montarozzi residuali a brughiera. La continuità della prateria è interrotta qua e là da *Betula pendula, Corylus avellana* e alberi caratteristici di boschi moderatamente termofili (*Quercus pubescens, Ostrya carpinifolia*).

Specificità: *Araneus alsine, Ero aphana, Ero furcata, Ceratinella scabrosa, Erigone autumnalis, Dipoena melanogaster*, Arctosa perita, Pardosa hortensis, Pardosa riparia, Nigma flavescens, Zelotes praeficus, Philodromus praedatus, Xysticus ninnii, Aelurillus v-insignitus, Marpissa nivoyi, Philaeus chrysops.*

Stazione 6: Superfici prative lungo il sentiero della "Cresta occidentale" che dall'edificio dell'ex sanatorio sale alla vetta, partendo da una quota di circa 750 m, esp. S. Prateria con parziale affioramento roccioso. All'inizio appare fortemente cespugliata e in via di chiusura, con forte influsso dell'elemento prenemorale verso un *Quercetum pubescentis* s.l.; più in alto dominano i molinieti e i seslerieti.

Specificità: *Lepthyphantes tenuis, Peponocranium orbiculatum, Salticus scenicus.*

Stazione 7: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 275 m, esp. NW. Superficie prativa terrazzata all'interno del bosco mesofilo, molto simile a quella della stazione 8 ma più aperta e con qualche elemento in più di *Mesobromion*.

Specificità: *Lepthyphantes flavipes**,

Stazione 8: Località Fornaci Villa, in prossimità dell'impluvio della Val Faè, 305 m, esp. NW. Superficie terrazzata, irregolarmente gestita e contornata da un bosco con notevoli contrassegni mesofili, in conseguenza dell'esposizione fresca e di un maggiore sviluppo del suolo.

Specificità: *Ozyptila rauda.*

Stazione 9: Località Ca' di Sala, 226 m, sulla riva settentrionale del bacino di Oggiono del Lago di Annone. Vi si evidenziano tre aspetti essenziali: 1) il canneto con accenni di aggruppamenti a *Iris pseudoacorus*, elementi di magnocariceto e residui di boscaglia ripariale. 2) il prato umido oligotrofico (*Molinion coeruleae*). 3) vegetazione erbacea perenne e disorganizzata, al margine superiore della stazione, riconducibile alle classi *Artemisietea vulgaris* e *Plantaginetea majoris*.

Specificità: *Tetragnatha extensa, Hypsosinga heri*, Gnathonarium dentatum*, Pardosa prativaga, Agelena labyrinthica, Clubiona phragmitis, Misumenops tricuspidatus, Runcinia lateralis, Xysticus ulmi.*

Elenco delle specie raccolte

In tale elenco si è seguito l'ordine adottato nella redazione della check-list delle specie italiane (Pesarini, 1995). Si è quindi seguito un ordine sistematico nella trattazione delle varie famiglie, mentre all'interno di ogni singola famiglia le specie vengono elencate in ordine alfabetico.

Si è colta l'occasione, per alcune specie, di fornire illustrazioni degli organi genitali, sempre molto utili per l'identificazione, quando di tali organi non è agevolmente disponibile, in letteratura, un'iconografia adeguata. Gli esemplari raffigurati, salvo contraria indicazione, provengono dalle raccolte effettuate nell'area del M. Barro.

Atypidae

Atypus affinis (Sulzer)

Corotipo: europeo (EUR).

Presenza in Italia: Lombardia e Toscana.

Un esemplare giovanile raccolto nell'alneto lungo il torrente della Val Faè (14.III.1990, lg. Aureggi).

Dysderidae

Dasumia taeniifera Thorell

Corotipo: Alpino appenninico.

Presenza in Italia: Lombardia, Emilia-Romagna, Toscana, Lazio.

Alcune ♀♀ raccolte nelle staz. 2 e 5.

Tetragnathidae

Pachygnatha clercki (Sundevall)

Corotipo: Sibirico-Europeo (SIE).

Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Calabria.

Un ♂ raccolto nell'alneto lungo il torrente della Val Faè (14.III.1990, lg. Aureggi).

Pachygnatha degeeri (Sundevall)

Corotipo: Paleartico (PAL).

Presenza in Italia: Liguria, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Umbria, Lazio, Campania, Calabria.

Alcuni esemplari raccolti nelle staz. 2 e 5 e nei boschi della Val Faè.

Tetragnatha extensa (Linneo)

Corotipo: Olartico (OLA).

Presenza in Italia: tutta Italia, Sicilia, Sardegna.

2 ♂♂ e 3 ♀♀ raccolti nella staz. 9.

Metidae

Meta segmentata (Clerck)

Corotipo: Paleartico (PAL).

Presenza in Italia: tutta Italia, Sicilia, Sardegna.

Numerosi esemplari raccolti nelle staz. 3, 5 e 7, nei boschi della Val Faè e nella zona ad Ovest dei Piani di Barra.

Araneidae

Aculepeira ceropegia (Walckenaer)

Corotipo: Paleartico (PAL).

Presenza in Italia: gran parte d'Italia, Sicilia, Sardegna.

Un esemplare giovanile raccolto nella staz. 2 (12.VI.1991, lg. Aureggi).

Agalenatea redii (Scopoli)

Corotipo: Paleartico (PAL).

Presenza in Italia: tutta Italia, Sicilia, Sardegna.

Alcune ♀♀ raccolte nelle staz. 2 e 5 e un esem-

plare giovanile raccolto nell'alneto lungo il torrente della val Faè.

Araneus alsine (Walckenaer)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Veneto.
Una ♀ raccolta nella staz. 5 (20.IX.1989, lg. Auriggi).

Araneus sturmi (Hahn)
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Toscana, Lazio, Campania, Puglia, Calabria.
Un ♂ raccolto nella staz. 3 (13.IX.1990, lg. Leonardi).

Araneus triguttatus (Fabricius)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Umbria, Lazio, Abruzzi.
Un ♂ raccolto nella staz. 3 (13.IX.1990, lg. Leonardi).

Araniella cucurbitina (Clerck)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Alcuni esemplari raccolti nelle staz. 2, 5 e 6.

Argiope bruennichi (Scopoli)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Alcuni esemplari, per lo più giovanili, raccolti nelle staz. 5 e 6 ed in prossimità dell'Osservatorio ornitologico.

Cercidia prominens (Westring)
Corotipo: Olartico (OLA).
Presenza in Italia: Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Toscana, Umbria, Abruzzi, Puglia, Calabria, Sardegna.
Alcuni esemplari raccolti nelle staz. 5 e 8 e nei boschi della Val Faè.

Cyclosa conica (Pallas)
Corotipo: Olartico (OLA).
Presenza in Italia: Tutta Italia, Sicilia, Sardegna.
Alcuni esemplari raccolti nelle stazioni 2 e 5 e 1 ♀ raccolta nei boschi della val Faè (23.V.1991 lg. Sassi).

Gibbaranea bituberculata (Walckenaer)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 2, 3, 5, 6 e 7 e nei boschi della Val Faè.

Hypsosinga heri (Hahn)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Umbria, Calabria, Sicilia.
Alcuni esemplari raccolti nella staz. 9 e nei boschi della Val Faè.

Hypsosinga sanguinea (Koch)
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Lazio, Calabria. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle stazioni 4 e 5.

Larinioides cornutus (Clerck)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Alcuni esemplari raccolti nelle stazioni 4 e 9.

Mangora acalypha (Walckenaer)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosissimi esemplari raccolti nelle staz. 2, 3, 5, 6, 7 e 9, nei boschi della Val Faè, presso l'Osservatorio ornitologico e ad Ovest dei Piani di Barra.

Neoscona adiantum (Walckenaer)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 2, 5, 6 e 9 e nei pressi dell'Osservatorio ornitologico.

Zilla diodia (Walckenaer)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Alcuni esemplari raccolti nelle staz. 5 e 6 e ad Ovest dei Piani di Barra.

Mimetidae

Ero aphana (Walckenaer)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Umbria, Calabria.
Un esemplare giovanile raccolto nella staz. 5 (23.V.1991, lg. Auriggi).

Ero furcata (Villers)
Corotipo: Europeo (EUR).
Presenza in Italia: Lombardia, Trentino-Alto Adige, Toscana.
Una ♀ raccolta nella staz. 5 (28.V.1990, lg. Aureggi).

Linyphiidae

Ceratinella scabrosa (Pickard-Cambridge)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: da me recentemente indicata, sulla scorta del presente reperto, in occasione della compilazione della check-list delle specie italiane dell'ordine (Pesarini 1995).
Un ♂ raccolto nella staz. 5 (28.V.1990, lg. Aureggi).
Osservazioni: il presente reperto è l'unico noto per la fauna italiana.

Cresmatoneta mutinensis (Canestrini), Fig. 1, 2
Corotipo: S-Europeo (SEU).
Presenza in Italia: Liguria, Lombardia, Emilia-Romagna, Toscana, Umbria, Puglia, Calabria.
Alcuni esemplari raccolti nelle stazioni 3 e 9.

Erigone autumnalis Emerton
Corotipo: Olartico (OLA).
Presenza in Italia: da me recentemente indicata, sulla scorta del presente reperto, in occasione della compilazione della check-list delle specie italiane dell'ordine (Pesarini 1995).
2 ♂♂ raccolti nella stazione 3 (10.VI.1991) e 5 ♂♂ raccolti nella staz. 5 (30.V.1989, lg. Leonardi).
Osservazioni: fino a pochi anni fa, questa specie era nota solo della fauna neartica; di recente Hänggi

(1990) l'ha segnalata del Canton Ticino (M. Generoso e M. S.Giorgio), quindi di un'area assai prossima al M. Barro. Sembrerebbe peraltro verosimile che l'effettiva diffusione della specie in Europa, pur se tuttora pressoché ignota, sia notevolmente più ampia.

Erigone dentipalpis (Wider)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Lazio, Campania.
Alcuni esemplari raccolti nelle staz. 5 e 9 e nell'alneto lungo il torrente della Val Faè.

Gnathonarium dentatum (Wider)
Corotipo: Paleartico (PAL).
Presenza in Italia: Piemonte, Friuli-Venezia Giulia, Emilia-Romagna, Toscana. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nella staz. 9 e nell'alneto lungo il torrente della Val Faè.

Hylyphantes nigritus (Simon)
Corotipo: Europeo (EUR).
Presenza in Italia: Piemonte, Friuli-Venezia Giulia, Toscana. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2 e 9 e nell'alneto lungo il torrente della Val Faè.

Lepthyphantes flavipes (Blackwall)
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino-Alto Adige, Campania.
Alcuni esemplari raccolti nella staz. 7 (3 ♂♂ e 9 ♀♀, 9.V.1990, lg. Aureggi) e nei boschi della Val Faè (1 ♀, 16.V.1990, lg. Aureggi).
Osservazioni: in realtà questa specie, che risulta nuova per la Lombardia, è assai comune e diffusa, almeno nell'Italia settentrionale, a dispetto dell'inspiegabile scarsità di precedenti segnalazioni.
Personalmente, mi è anche nota delle seguenti località: Liguria: Finale Ligure (15.V.88, lg. Sciaky, 1 ♂). Piemonte: Crissolo (30.IV.1983, lg. Sciaky, 1 ♀); Rovasenda (prov. Vercelli, VIII.1984, lg. Gozzi, 1 ♂). Lombardia: Dumenza (prov. Varese, 12.VII.1987, lg. Zanon, 1 ♀); Val Fredda (prov. Varese, 4.X.1983, lg. Baratelli, 1 ♀); Bernate Ticino (prov. Milano, XII.1989, I.1990, II.1990, lg. Pasquetto, 7 ♂♂ e 5 ♀♀); Monza Parco (IX.1985, lg. Sciaky, 1 ♂ e 2 ♀♀); Montorfano (prov. Brescia, II.1991, 4 ♂♂ e 6 ♀♀, lg. Ghilardi). Veneto: M. Cesen (prov. Treviso, 2.V.1988, lg. Zanon, 1 ♀); Col Perer (prov. Belluno, 25.VI.1988, lg. Zanon, 1 ♂ e 1 ♀); Cima di Campo (prov. Belluno, 25.VI.1988, 2 ♂♂ e 2 ♀♀). Friuli-Venezia Giulia: Grotta Ercole presso Gabrovizza (prov. Trieste, 18.VIII.1986, lg. Zanon, 1 ♀). Emilia- Romagna: Badagnano (prov. Piacenza, 24.III.1982, lg. Pavesi, 1 ♂).

Lepthyphantes tenuis (Blackwall)
Corotipo: Europeo (EUR).
Presenza in Italia: Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Marche, Lazio, Campania, Puglia, Calabria. La specie non risultava segnalata per la Lombardia.
Una ♀ raccolta nella staz. 6 (11.VI.1990, lg. Aureggi)

Linyphia hortensis Sundevall
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Marche, Campania, Calabria.
Numerosi esemplari raccolti nelle staz. 2, 3, 5 e 6 e nei boschi della Val Faè.

Meioneta rurestris (Koch)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Puglia. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nella staz. 3 (14.III.1990, lg. Leonardi).

Microlinyphia pusilla (Sundevall)
Corotipo: Olartico (OLA).
Presenza in Italia: Italia Settentrionale, Emilia-Romagna, Toscana, Umbria, Calabria.
Alcuni esemplari raccolti nelle staz. 2, 3 e 5, nell'alneto lungo il torrente della Val Faè e presso l'Osservatorio ornitologico.

Minicia marginella (Wider)
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino-Alto Adige. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2, 5, 6 e 9 e ad Ovest dei Piani di Barra.

Nematogmus sanguinolentus (Walckenaer)
Corotipo: Europeo (EUR).
Presenza in Italia: Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Toscana, Lazio, Puglia.
Alcuni esemplari raccolti nelle staz. 3, 6 e 9 e presso l'Osservatorio ornitologico.

Neriene peltata (Wider)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Campania, Puglia, Calabria. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nei boschi della Val Faè (16.V.1990, lg. Aureggi).

Peponocranium orbiculatum (Pickard-Cambridge)
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino-Alto Adige. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nella staz. 6 (11.VI.1990, lg. Aureggi).

Porrhomma pygmaeum (Blackwall)
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: Veneto. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nella staz. 2 (23.V.1991, lg. Aureggi).

Walckenaeria antica (Wider)
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino-Alto Adige. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2, 3, 4 e 7.

Fig. 1-4 - 1-2) *Cresmatoneta mutinensis* (Canestrini); 1) pedipalpo ♂ in visione laterale; 2) id., epigino ♀; 3-4) *Cheiracanthium elegans* Thorell; 3) pedipalpo ♂ in visione laterale; 4) *Cheiracanthium montanum* Koch, pedipalpo ♂ in visione laterale.

Theridiidae

Achaearanea lunata (Clerck)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Campania, Calabria, Sicilia.
Un ♂ raccolto ad Ovest dei Piani di Barra (25.VI.1991, lg. Aureggi).

Crustulina guttata (Wider)
Corotipo: Olartico (OLA).
Presenza in Italia: Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Campania, Puglia. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2, 4, 5 e 6.

Dipoena melanogaster (Koch)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Marche, Lazio, Italia meridionale, Sicilia. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nella staz. 5 e nei boschi della Val Faè.

Enoplognatha ovata (Clerck)
Corotipo: Olartico (OLA).
Presenza in Italia: Tutta Italia, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 2, 5 e 9, nei boschi della Val Faè e ad Ovest dei Piani di Barra.

Enoplognatha thoracica (Hahn)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: da me recentemente indicata in occasione della compilazione della check-list delle specie italiane dell'ordine (Pesarini, 1995).
Alcuni esemplari raccolti nelle stazioni 3 e 4 e un ♂ nei boschi della Val Faè (16.V.1990, lg. Aureggi).
Osservazioni: Questa specie, di cui non esistono in letteratura altre indicazioni per la fauna italiana, mi è comunque nota anche di un'altra località lombarda (Raffa del Garda in provincia di Brescia, 24.V.1991, un G, lg. Cauda), di Veneto (Ponte Florio in provincia di Verona, un G, lg. Ferri) e Sicilia (Torre Montaspro in provincia di Palermo, 4.VII.1991, 4 ♀♀, lg. Pesarini & Sabbadini).

Episinus truncatus Latreille
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Marche, Umbria, Campania, Calabria, Sardegna.
Alcuni esemplari raccolti nella staz. 2 e nei boschi della Val Faè.

Euryopis flavomaculata (Koch)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Umbria, Lazio, Campania. La specie risulta nuova per la Lombardia.
Un ♂ raccolto presso l'Osservatorio ornitologico (16.V.1990, lg. Aureggi).

Neottiura bimaculata (Linneo)
Corotipo: Sibirico-Europeo (SIE)
Presenza in Italia: Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Umbria, Lazio, Campania, Calabria, Sicilia.
Alcuni esemplari raccolti nelle staz. 2, 5 e 6, nei boschi della Val Faè e ad Ovest dei Piani di Barra.

Theridion nigrovariegatum Simon
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Emilia-Romagna, Marche, Campania, Calabria, Sicilia. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 5 e 6, presso l'Osservatorio ornitologico e ad Ovest dei Piani di Barra.

Theridion simile Koch
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Piemonte, Trentino-Alto Adige, Veneto, Friuli-Venezia Giulia, Toscana, Marche, Umbria, Lazio, Abruzzo, Campania, Basilicata, Calabria, Sicilia. La specie risulta nuova per la Lombardia e mi è nota anche di Emilia (Badagnano in provincia di Piacenza, diversi esemplari di diverse date, lg. Pavesi e Pesarini).
3 ♂♂ e 4 ♀♀ raccolti nelle stazioni 2, 5 e 6, lg. Bonini.

Pisauridae
Pisaura mirabilis (Clerck)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosissimi esemplari (fra cui però solamente 6 ♂♂ e 9 ♀♀ adulti) raccolti nelle staz. 1, 2, 3, 5, 6, 7, 8 e 9 e presso l'Osservatorio ornitologico.
Osservazioni: gli adulti rinvenuti sono da attribuire alla specie intesa in senso stretto, e non a qualcuna delle specie strettamente affini solo recentemente prese in considerazione nella letteratura; nessuna indicazione precisa in tal senso, ovviamente, può essere fornita per i numerosi giovani.

Lycosidae
Arctosa perita (Latreille)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale e centrale, Puglia, Calabria, Sardegna.
Un ♂ raccolto nella staz. 5 (28.V.1990, lg. Aureggi).

Aulonia albimana (Walckenaer)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana.
Alcuni esemplari raccolti nelle staz. 2 e 5.

Pardosa hortensis (Thorell)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Campania, Puglia, Basilicata, Calabria.
Un ♂ raccolto nella staz. 5 (28.V.1990, lg. Aureggi).

Pardosa lugubris (Walckenaer)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Campania, Puglia, Basilicata, Calabria.
Alcuni esemplari raccolti nelle staz. 5 e 6, nei boschi della Val Faè e presso l'Osservatorio ornitologico.

Pardosa prativaga (Koch)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Emilia-Romagna, Toscana, Campania, Calabria. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nella staz. 9 (15.VI.1990, lg. Leonardi).

Pardosa riparia (Koch)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Calabria.
Un ♂ proveniente dalla staz. 5 (23.V.1991, lg. Aureggi).

Trochosa ruricola (Degeer)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Umbria, Puglia, Calabria, Sicilia.
Alcuni esemplari raccolti nella staz. 2 e presso l'Osservarorio ornitologico.

Xerolycosa nemoralis (Westring)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Toscana, Calabria.
Alcuni esemplari raccolti nella staz. 2 e ad Ovest dei Piani di Barra.

Agelenidae
Agelena labyrinthica (Clerck)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Un esemplare giovanile raccolto nella staz. 9 (22.V.1991, lg. Leonardi).

Dyctinidae
Brigittea latens (Fabricius)
Corotipo: W-Paleartico (WPA).
Presenza in Italia: Piemonte, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Campania, Puglia, Calabria. La specie risulta nuova per la Lombardia.
5 ♀♀ raccolte nella staz. 2 (16.V.1991, lg. Aureggi).

Nigma flavescens (Walckenaer)
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Lombardia, Emilia-Romagna, Toscana, Lazio.
Un ♂ raccolto nella staz. 5 (25.VI.1991, lg. Aureggi).

Nigma puella (Simon)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Lombardia, Emilia-Romagna, Toscana, Umbria.
Una ♀ raccolta nei boschi della Val Faè (30.V.1990, lg. Aureggi).

Anyphaenidae
Anyphaena accentuata (Walckenaer)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sardegna.
Una ♀ raccolta nei boschi della Val Faè (16.V.1990, lg. Aureggi).

Clubionidae
Cheiracanthium elegans Thorell, Fig. 3
Corotipo: Europeo (EUR).
Presenza in Italia: Veneto, Emilia-Romagna, To-

scana, Lazio, Campania, Calabria. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nei sottoboschi della Val Faè (16.V.1990, lg. Leonardi).

Cheiracanthium montanum Koch, Fig. 4
Corotipo: Centroeuropeo (CEU).
Presenza in Italia: da me recentemente indicata, sulla scorta del presente reperto, in occasione della compilazione della check-list delle specie italiane dell'ordine (Pesarini 1995).
Un ♂ raccolto nella staz. 3 (9.V.1990, lg. Leonardi).

Clubiona neglecta Pickard-Cambridge
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Friuli-Venezia Giulia, Emilia-Romagna, Puglia. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nella staz. 2 (15.IV.1989, lg. Leonardi) e una ♀ nella staz. 6 (12.VI.1991, lg. Aureggi).

Clubiona phragmitis Koch
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Umbria, Marche, Basilicata.
Un ♂ e una ♀ raccolti nella staz. 9 (11.VI.1991, lg. Aureggi).

Clubiona terrestris Westring
Corotipo: Europeo (EUR).
Presenza in Italia: Liguria, Veneto, Trentino-Alto Adige, Umbria, Lazio, Campania, Calabria. La specie risulta nuova per la Lombardia.
Un ♂ raccolto nella staz. 1 (10.VI.1991, lg. Leonardi) e una ♀ raccolta nei boschi della Val Faè (16.V.1990, lg. Aureggi).

Gnaphosidae
Zelotes praeficus (Koch)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Calabria. La specie risulta nuova per la Lombardia.
Un ♂ raccolto nella staz. 5 (28.V.1990, lg. Aureggi).

Eusparassidae
Micrommata virescens (Clerck)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Italia settentrionale e centrale, Campania, Calabria, Sardegna.
Nunerosi esemplari, in prevalenza giovanili, raccolti nelle staz. 2, 5, 7 e 9, nei boschi della Val Faè e presso l'Osservatorio ornitologico.

Philodromidae
Philodromus aureolus (Clerck)
Corotipo: Olartico (OLA).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Emilia-Romagna, Marche, Campania, Puglia, Calabria, Sicilia.
Alcuni esemplari raccolti nelle staz. 5, 6 e 9.

Philodromus cespitum (Walckenaer)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Lazio, Campania, Puglia, Sicilia. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 6 e 9.

Philodromus dispar Walckenaer
Corotipo: Europeo (EUR).
Presenza in Italia: Emilia-Romagna, Umbria, Lazio. La specie risulta nuova per la Lombardia.
Numerosi esemplari raccolti nelle staz. 3, 5, 7 e 8 e nei boschi della Val Faè.

Philodromus praedatus Pickard-Cambridge
Corotipo: Europeo (EUR).
Presenza in Italia: da me recentemente indicata in occasione della compilazione della check-list delle specie italiane dell'ordine (Pesarini 1995).
Una ♀ raccolta nella staz. 5 (28.V.1990, lg. Aureggi).
Osservazioni: solo recentemente rivalutata, questa specie non risultava precedentemente segnalata d'Italia, dove è in realtà abbastanza diffusa; oltre che del M. Barro mi è infatti nota delle seguenti località: Piemonte: Roncasso (prov. Torino, VII.1981, lg. Giachino, 1 ♀). Lombardia: Piazzatorre (prov. Bergamo, 14.IX.1989, lg. Carnelli, 1 ♀). Basilicata: M. Pollino (prov. Potenza, VI.1991, lg. Sabbadini, 1 ♀). Sicilia: Piano Zucchi (prov. Palermo, 2/4.VII.1991, lg. Pesarini & Sabbadini, 2 ♀♀).

Tibellus oblongus (Walckenaer)
Corotipo: Olartico (OLA).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Lazio, Campania, Calabria.
Alcuni esemplari raccolti nelle staz. 2, 3, 5, 6 e 9 e nei dintorni dell'Osservatorio ornitologico.

Thomisidae
Heriaeus hirtus (Latreille)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Emilia-Romagna, Toscana, Umbria, Campania, Puglia, Calabria, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 2, 5 e 6, nei boschi della Val Faè e presso l'Osservatorio ornitologico.

Misumena vatia (Clerck)
Corotipo: Olartico (OLA).
Presenza in Italia: tutta Italia, Sicilia.
Numerosi esemplari raccolti nelle staz. 2, 3, 5, 6, 7, 8 e 9, nei boschi della Val Faè, presso l'Osservatorio ornitologico e ad Ovest dei Piani di Barra.

Misumenops tricuspidatus (Fabricius)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Liguria, Piemonte, Lombardia, Veneto, Emilia-Romagna, Toscana.
Numerosi esemplari raccolti in maggio e giugno nella staz. 9.

Ozyptila rauda Simon
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Friuli-Venezia Giu-

lia, Emilia-Romagna, Puglia. La specie risulta nuova per la Lombardia.
Un ♂ raccolto nella staz. 8 (16.V.1990, lg. Aureggi).

Runcinia lateralis (Koch)
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale e centrale, Calabria, Sicilia, Sardegna.
Numerosi esemplari raccolti nella staz. 9 in maggio e giugno.

Synaema globosum (Fabricius)
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 1, 2, 3, 6 e 9, nei boschi della Val Faè, presso l'Osservatorio ornitologico e ad Ovest dei Piani di Barra.

Thomisus onustus Walckenaer
Corotipo: Paleartico (PAL).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 2, 5 e 6, ad Ovest dei Piani di Barra e presso l'Osservatorio ornitologico.

Tmarus piger (Walckenaer)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Italia settentrionale e centrale, Campania.
Numerosi esemplari raccolti nelle staz. 2, 3, 5, 6, 7 e 8, nei boschi della Val Faè e presso l'Osservatorio ornitologico.

Xysticus acerbus Thorell
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Lombardia, Veneto, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Sicilia.
Alcuni esemplari raccolti nelle staz. 2 e 5 e presso l'Osservatorio ornitologico.

Xysticus audax (Schrank)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Lazio, Campania, Calabria, Sardegna.
Alcuni esemplari raccolti nelle staz. 2 e 5.

Xysticus bifasciatus Koch
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Emilia-Romagna, Basilicata, Sardegna.
Alcuni esemplari raccolti nelle staz. 2, 5 e 6.

Xysticus bufo (Dufour)
Corotipo: Mediterraneo (MED).
Presenza in Italia: Liguria, Piemonte, Lombardia, Toscana, Lazio.
Alcuni esemplari raccolti nella staz. 2 e nell'alneto lungo il torrente della Val Faè.

Xysticus cristatus (Clerck)
Corotipo: Paleartico (PAL).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Marche, Campania, Calabria, Sardegna.
Numerosissimi esemplari raccolti nelle staz. 2, 3, 5 e 6 e ad Ovest dei Piani di Barra.

Xysticus erraticus (Blackwall)
Corotipo: Europeo (EUR).
Presenza in Italia: Trentino-Alto Adige. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2 e 5.

Xysticus kempeleni Thorell
Corotipo: Europeo (EUR).
Presenza in Italia: Veneto, Friuli-Venezia Giulia, Emilia-Romagna. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2, 3, 5 e 7.

Xysticus kochi Thorell
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sardegna.
Alcuni esemplari raccolti nelle staz. 2, 3, 5, 6 e 9, nei boschi della Val Faè e nell'alneto lungo il torrente della Val Faè.

Xysticus lanio Koch
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana.
Alcuni esemplari raccolti nelle staz. 2, 5, 7, 8 e 9, nei boschi della Val Faè, nell'alneto lungo il torrente della Val Faè e ad Ovest dei Piani di Barra.

Xysticus ninnii Thorell
Corotipo: W.Paleartico (WPA).
Presenza in Italia: Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Basilicata. La specie risulta nuova per la Lombardia.
Un ♂ raccolto nella staz. 5 (28.V.1990, lg. Aureggi).

Xysticus ulmi (Hahn)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Lombardia, Veneto, Trentino-Alto Adige, Marche, Calabria.
2 ♂♂ e 2 ♀♀ raccolti nella staz. 9 (15.VI.1990, lg. Leonardi).

Salticidae

Aelurillus v-insignitus (Clerck)
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Basilicata, Calabria, Sardegna.
Un ♂ raccolto nella staz. 5 (25.VI.1991, lg. Aureggi).

Ballus depressus (Walckenaer)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Alcuni esemplari raccolti nelle staz. 1, 2, 5 e 6, nei boschi della Val Faè, presso l'Osservatorio ornitologico e ad Ovest dei Piani di Barra.

Bianor aurocinctus (Ohlert)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: Liguria, Veneto, Trentino-Alto Adige. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 1, 2, 5 e 6 e ad Ovest dei Piani di Barra.

Eris nidicolens (Walckenaer), Fig. 5
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Liguria, Lombardia, Veneto, Trentino-Alto-Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Marche, Umbria, Campania, Puglia, Calabria, Sardegna.
Alcuni esemplari raccolti nelle staz. 2, 4 e 5.

Heliophanus aeneus (Hahn)
Corotipo: Centroasiatico-Europeo (CAE).
Presenza in Italia: Italia settentrionale, Toscana, Calabria, Sicilia.
Una ♀ raccolta nella staz. 2 (23.V.1991, lg. Leonardi).

Heliophanus auratus Koch
Corotipo: Sibirico-Europeo (SIE).
Presenza in Italia: Piemonte, Val d'Aosta, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Sardegna. La specie risulta nuova per la Lombardia.
Alcuni esemplari raccolti nelle staz. 2, 5 e presso l'Osservatorio ornitologico.

Heliophanus cupreus (Walckenaer)
Corotipo: Europeo (EUR).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Numerosissimi esemplari raccolti in tutti gli ambienti indagati eccetto la staz. 1.
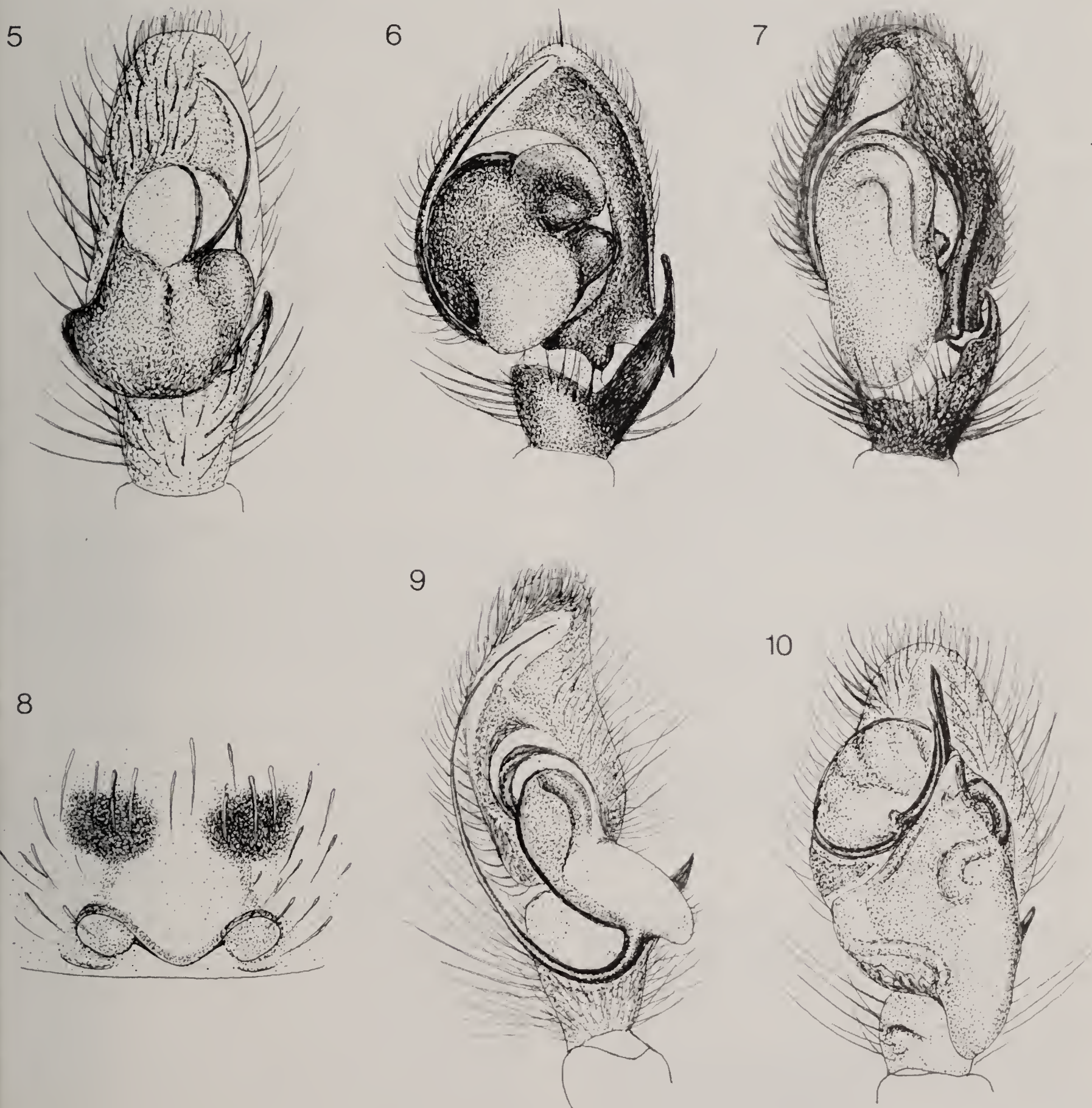
Fig. 5-10 - 5) *Eris nidicolens* (Walckenaer), pedipalpo ♂ in visione ventrale. 6) *Marpissa nivoyi* (Lucas), pedipalpo ♂ in visione ventrale; 7) *Mithion canestrinii* (Ninni), pedipalpo ♂ in visione ventrale; 8) id., epigino ♀; 9) *Philaeus chrysops* (Poda), pedipalpo ♂ in visione ventrale; 10) *Saitis barbipes* (Simon), pedipalpo ♂ in visione ventrale.

Heliophanus flavipes (Hahn)
Corotipo: Asiatico-Europeo (ASE).
Presenza in Italia: Lombardia, Veneto, Trentino-Alto Adige, Friuli-Venezia Giulia, Emilia-Romagna, Toscana, Umbria, Lazio, Italia meridionale, Sicilia, Sardegna.
Numerosi esemplari raccolti nelle staz. 2, 3, 4, 5, 6 e 9, nei boschi della Val Faè e presso l'Osservatorio ornitologico.

Heliophanus kochi Simon
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Italia settentrionale e centrale, Puglia, Calabria, Sardegna.
Alcuni esemplari raccolti nelle staz. 1 e 3, 4 e 5.

Marpissa nivoyi (Lucas), Fig. 6
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: Liguria, Emilia-Romagna, Toscana, Umbria, Lazio, Campania. La specie risulta nuova per la Lombardia.
Una ♀ raccolta nella staz. 5 (15.IV.1989, lg. Leonardi).

Mithion canestrinii (Ninni), Fig. 7, 8 e 11
Corotipo: europeo (EUR).
Presenza in Italia: Veneto, Emilia-Romagna, Umbria, Basilicata, Sicilia, Sardegna. La specie risulta nuova per la Lombardia.
Numerosi esemplari (14 ♂♂, 11 ♀♀ e 11 immaturi) raccolti nella staz. 9 (15.VI.1990, lg. Leonardi), altri esemplari nelle stazioni 4 e 5.
Osservazioni: il genere *Mithion* Simon, comprendente la qui presente specie come unico rappresentante, viene generalmente considerato, nella letteratura più recente, sinonimo di *Marpissa*. Le differenze molto nette che si riscontrano nei genitali dei due sessi fra le varie specie di *Marpissa* da una lato, e la presente specie dall'altro, mi inducono a ritenere ingiustificato il declassamento di *Mithion*, che preferisco continuare a trattare alla stregua di genere a sé stante.

Myrmarachne formicaria (Degeer)
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Calabria, Sicilia, Sardegna.
Alcuni esemplari raccolti nelle staz. 2, 3, 6 e 9.

Philaeus chrysops (Poda), Fig. 9
Corotipo: Europeo-Mediterraneo (EUM).
Presenza in Italia: tutta Italia, Sicilia, Sardegna.
Un ♂ raccolto nella staz. 5 (25.VI.1991, lg. Aureggi).

Saitis barbipes (Simon), Fig. 10
Corotipo: Europeo (EUR).
Presenza in Italia: Italia settentrionale e centrale, Campania, Calabria.
Alcuni esemplari raccolti nei boschi della Val Faè e ad Ovest dei Piani di Barra.

Salticus scenicus (Clerck)
Corotipo: Olartico (OLA).
Presenza in Italia: Italia settentrionale, Emilia-Romagna, Toscana, Umbria, Campania, Puglia, Calabria, Sicilia, Sardegna.
Un ♂ e una ♀ raccolti nella staz. 6 (12.VI.1991, lg. Aureggi).
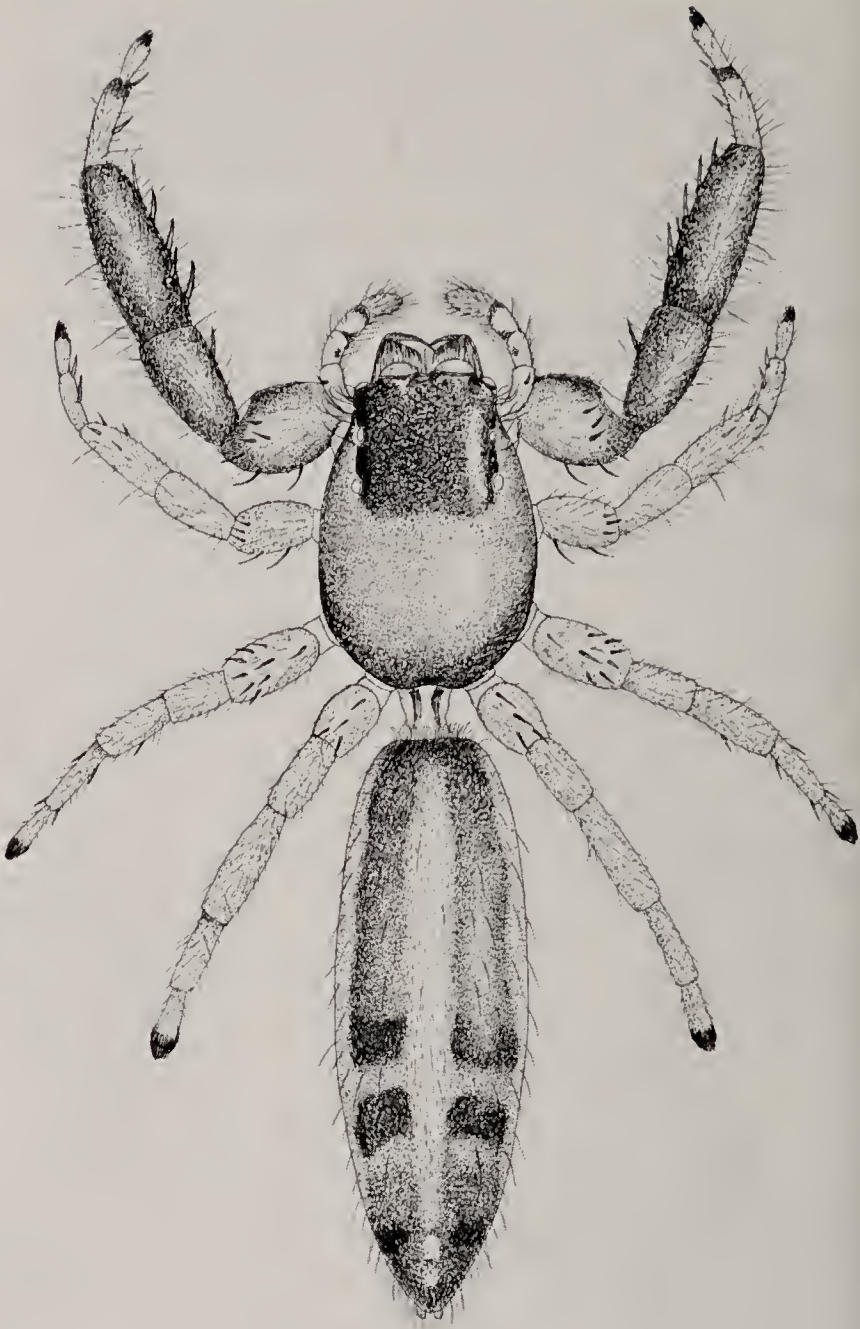
Fig. 11 - *Mithion canestrinii* (Ninni), ♀, habitus.

Nella seguente tabella (Tabella 1) sono riuniti i dati relativi alla presenza delle specie nelle diverse stazioni. Tutte le stazioni successive alla nona sono riunite nel numero 10. Si tratta per lo più di località situate nei boschi della Val Faè; indicazioni più dettagliate, peraltro, si possono ricavare dalla precedente trattazione delle singole specie.

Tabella 1 - Tabella riassuntiva delle specie raccolte.

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Atypus affinis										+
Dasumia taeniifera		+			+					
Pachygnatha clercki										+
Pachygnatha degeeri		+	+		+					+
Tetragnatha extensa									+	
Meta segmentata			+		+		+			+
Aculepeira ceropegia		+								
Agalenatea redii		+			+					+
Araneus alsine					+					
Araneus sturmi			+							
Araneus triguttatus			+							
Araniella cucurbitina		+			+	+				
Argiope bruennichi					+	+				+

Specie	Stazioni									
	1	2	3	4	5	6	7	8	9	10
Cercidia prominens					+			+		+
Cyclosa conica		+			+					+
Gibbaranea bituberculata		+	+		+	+	+			+
Hypsosinga heri									+	+
Hypsosinga sanguinea				+	+					
Larinioides cornutus				+					+	
Mangora acalypha		+	+		+	+	+		+	+
Neoscona adiantum		+			+	+			+	+
Zilla diodia					+	+				+
Ero aphana					+					
Ero furcata					+					
Ceratinella scabrosa					+					
Cresmatoneta mutinensis			+						+	
Erigone autumnalis			+		+					
Erigone dentipalpis					+				+	+
Gnathonarium dentatum									+	+
Hylyphantes nigritus		+							+	+
Lepthyphantes flavipes							+			+
Lepthyphantes tenuis						+				
Linyphia hortensis		+	+		+	+				+
Meioneta rurestris			+							
Microlinyphia pusilla		+	+		+					+
Minicia marginella		+			+	+			+	+
Nematogmus sanguinolentus			+			+			+	+
Neriene peltata										+
Peponocranium orbiculatum						+				
Porrhomma pygmaeum			+							
Walckenaeria antica		+	+	+			+			
Achaearanea lunata										+
Crustulina guttata		+		+	+	+				
Dipoena melanogaster					+					+
Enoplognatha ovata		+			+				+	+
Enoplognatha thoracica			+	+						+
Episinus truncatus		+								+
Euryopis flavomaculata										+
Neottiura bimaculata		+			+	+				+
Theridion nigrovariegatum					+	+				
Theridion simile		+			+	+				
Pisaura mirabilis	+	+	+		+	+	+	+	+	+
Arctosa perita					+					
Aulonia albimana		+			+					
Pardosa hortensis					+					
Pardosa lugubris					+	+				+
Pardosa prativaga									+	
Pardosa riparia					+					
Trochosa ruricola		+								+
Xerolycosa nemoralis		+								+
Agelena labyrinthica									+	
Brigittea latens		+								
Nigma flavescens					+					
Nigma puella										+
Anyphaena accentuata										+
Cheiracanthium elegans										+
Cheiracanthium montanum			+							
Clubiona neglecta		+				+				
Clubiona phragmitis									+	
Clubiona terrestris	+									+
Zelotes praeficus					+					
Micrommata virescens		+			+		+		+	+
Philodromus aureolus					+	+			+	
Philodromus cespitum						+			+	
Philodromus dispar			+		+		+	+		+
Philodromus praedatus					+					
Tibellus oblongus		+	+		+	+			+	+
Heriaeus hirtus		+			+	+				+
Misumena vatia		+	+		+	+	+	+	+	+
Misumenops tricuspidatus									+	
Ozyptila rauda								+		
Runcinia lateralis									+	
Synaema globosum	+	+	+			+			+	+
Thomisus onustus		+			+	+				+
Tmarus piger		+	+		+	+	+	+		+
Xysticus acerbus		+			+					+
Xysticus audax		+			+					
Xysticus bifasciatus		+			+	+				
Xysticus bufo		+								+
Xysticus cristatus		+	+		+	+				+
Xysticus erraticus		+			+					
Xysticus kempeleni		+	+		+		+			
Xysticus kochi		+	+		+	+			+	+
Xysticus lanio		+			+		+	+	+	+
Xysticus ninnii					+					
Xysticus ulmi									+	
Aelurillus v-insignitus					+					
Ballus depressus	+	+			+	+				+
Bianor aurocinctus	+	+			+	+				+
Eris nidicolens		+		+	+					
Heliophanus aeneus		+								
Heliophanus auratus		+			+					+
Heliophanus cupreus		+	+	+	+	+	+	+	+	+
Heliophanus flavipes		+	+	+	+	+			+	+
Heliophanus kochi	+		+	+	+					
Marpissa nivoyi					+					
Mithion canestrinii				+	+				+	
Myrmarachne formicaria			+	+		+			+	
Philaeus chrysops					+					
Saitis barbipes										+
Salticus scenicus						+				

Considerazioni conclusive

Le ricerche condotte nell'area del Monte Barro hanno condotto al rinvenimento di 111 specie di ragni, pari al 7,89 per cento della fauna italiana complessiva; un raffronto fra la fauna censita e quella italiana è messa in evidenza nella tabella 2, dove per ciascuna famiglia vengono indicati i dati sottospecificati, relativi alla ricerca condotta sul Monte Barro (lettere minuscole) e relativi all'intera fauna italiana (lettere maiuscole).

Tabella 2 - Numero di specie delle singole famiglie raccolte sul Monte Barro (a) e note per l'intero territorio italiano (A), e relative percentuali (b, B) riferite al numero totale di specie della fauna araneologica

	a	A	b	B	b/B
Atypidae	1	3	0,90	0,21	4,29
Dysderidae	1	61	0,90	4,34	0,21
Tetragnathidae	3	12	2,70	0,85	3,18
Metidae	1	6	0,90	0,43	2,09
Araneidae	16	60	14,41	4,27	3,37
Mimetidae	2	6	1,80	0,43	4,19
Linyphiidae	17	382	15,32	27,17	0,56
Theridiidae	10	101	9,01	7,18	1,25
Pisauridae	1	6	0,90	0,43	2,09
Lycosidae	8	91	7,21	6,47	1,11
Agelenidae	1	75	0,90	5,33	0,17
Dictynidae	3	22	2,70	1,56	1,73
Anyphaenidae	1	3	0,90	0,21	4,29
Clubionidae	5	43	4,50	3,06	1,47
Gnaphosidae	1	143	0,90	10,17	0,09
Eusparassidae	1	5	0,90	0,36	2,50
Philodromidae	5	25	4,50	1,78	2,53
Thomisidae	19	67	17,12	4,77	3,59
Salticidae	15	135	13,51	9,60	1,41

In ricerche condotte in aree sufficientemente diversificate, come è il caso dell'area del Monte Barro, il rapporto b/B, per famiglie discretamente vaste (comprendenti almeno una trentina di specie) è generalmente compreso fra 0,5 e 2, con tendenza al limite inferiore per le famiglie comprendenti numerose specie a distribuzione geografica ristretta ed a quello superiore per famiglie con specie in prevalenza a distribuzione ampia. Il rapporto b/B tende inoltre a discostarsi più o meno nettamente dall'unità in un senso o nell'altro (a seconda delle caratteristiche geografiche o ecologiche dell'ambiente) nel caso di famiglie comprendenti numerose specie stenoecie o a distribuzione geografica marcatamente caratterizzata. Nel caso della presente ricerca, si può notare che i limiti indicati vengono in alcuni casi largamente superati nei due sensi, per eccesso nel caso di Thomisidae (3,59) e Araneidae (3,16), per difetto nel caso di Dysderidae (0,21), Agelenidae (0,17) e Gnaphosidae (0,09). I fattori precedentemente indicati hanno contribuito in parte al discostamento dall'unità (Araneidae e Thomisidae comprendono numerose specie a diffusione geografica molto ampia, mentre Dysderidae, Agelenidae e Gnaphosidae comprendono numerose specie a diffusione ristretta e/o a gravitazione mediterranea), ma il netto superamento dei limiti mediamente riscontrati è senz'altro da attribuirsi alle modalità di ricerca, che hanno fornito un quadro sufficientemente completo delle specie diurne legate alla vegetazione (come appunto Thomisidae ed Araneidae), mentre è pressoché sicuro che numerose specie di Dysderidae, Agelenidae e soprattutto Gnaphosidae (terricole e spesso a costumi notturni) siano sfuggite alle ricerche, che in tal caso hanno fornito un quadro della popolazione araneologica nettamente sbilanciato a sfavore di questi ultimi taxa. Nonostante queste limitazioni, peraltro, i dati geonemici ottenuti con la presente ricerca sono comunque di notevole interesse, anche in considerazione dell'estrema lacunosità delle attuali conoscenze sulla fauna araneologica italiana: ben 5 specie risultavano infatti non ancora segnalate per la fauna italiana, e addirittura 32 nuove per la fauna lombarda.

Indicazioni sulle caratteristiche ambientali sono fornite dalla sottoindicata tabella corologica del popolamento censito (tabella 3), che fornisce un quadro di ambiente mesotermo, con elementi criofili in leggera maggioranza rispetto a quelli termofili e con un'ampia componente di specie euriecie.

Tabella 3 - Spettro corologico delle specie raccolte. Le sigle dei corotipi fondamentali sono ricavate dal lavoro di Vigna et al. (1991).

Corotipo	n° specie	% sul totale
Europeo (EUR)	27	24,32
Sibirico-Europeo (SIE)	22	19,82
Europeo-Mediterranee (EUM)	18	16,22
Paleartico (PAL)	13	11,71
Olartico (OLA)	11	9,91
Asiatico-Europeo (ASE)	8	7,21
Centroasiatico-Europeo (CAE)	4	3,60
W-Paleartico (WPA)	3	2,70
Centroeuropeo (CEU)	3	2,70
Alpino-Appenninico	1	0,90
S-Europeo (SEU)	1	0,90

La figura 12, dove i corotipi sono raggruppati per categorie sintetiche, visualizza la dominanza di elementi ad ampia distribuzione (oltre il 70% delle specie raccolte) e la totale assenza di elementi mediterranei.
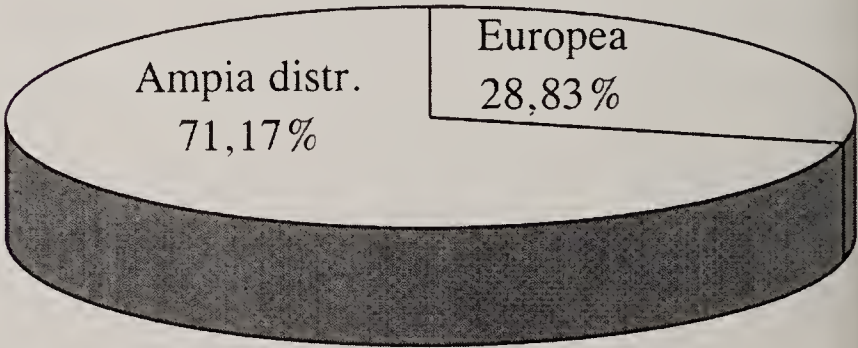
Fig. 12 - Corotipi raggruppati per categorie sintetiche.

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